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An international journal to expedite plant systematic, phytogeographical
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Phytologia (March 1990) 68(3):157-159.NEW YORK
BOTANICAL GARDENA NEW SPECIES OF *SABAZIA* (ASTERACEAE: HELIANTHEAE)
FROM OAXACA, MÉXICO

B.L. Turner

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

Sabazia macdonaldii B. Turner, from the subalpine region of Cerro Quiexobra, Oaxaca, México, is described and illustrated. It is closely related to *S. multiradiata* (Seaton) Longpre, but differs in having pilose foliage and larger heads.

KEY WORDS: *Sabazia*, Asteraceae, Heliantheae, taxonomy, neotropical flora, México.

Collections from Cerro Quiexobra, Oaxaca, México, have revealed the following novelty. It is closely related to *Sabazia multiradiata*, possessing the nearly sessile leaves of that species, but differs in having pilose foliage and larger heads.

Sabazia macdonaldii B. Turner, *sp. nov.*, Figure 1. TYPE: MÉXICO. Oaxaca: 35 km ESE of Miahuatlán, 5-10 km NE of Santo Domingo Ozolotepec, Cerro Quiexobra, (16° 10' N, 96° 15' W), 3200-3500 m, 11 Dec 1989, Andrew McDonald 2952 (HOLOTYPE: TEX; Isotype: MEXU).

Sabazia multiradiata (Seaton) Longpre similis sed capitulis majoribus involucris 7-9 mm altis (vs 4-7 mm) et caulibus et foliis pilosis trichomatibus plerumque 1-2 mm longis differt.

Perennial herbs 20-30 cm high. Stems erect, arising from slender rhizomes, spreading pilose below, less so above. Leaves opposite, 3-5 pairs per stem; petioles 1-2 mm long, pilose; blades ovate, mostly 3-4 cm long, 1-2 cm wide, 3 nervate from somewhat above the acute to obtuse base, pilose on both surfaces with hairs mostly 1.0-1.5 mm long, the margins serrate to nearly entire. Heads on peduncles 5-15 cm long, ca 3 cm wide across the extended rays. Involucres broadly campanulate, 7-9 mm high, 10-15 mm wide, the bracts subequal, 2-3 seriate. Receptacle conical, the pales ovate-lanceolate, scarious and somewhat 3 lobed. Ray florets 8, pistillate, fertile, the ligules white, 10-15 mm long,

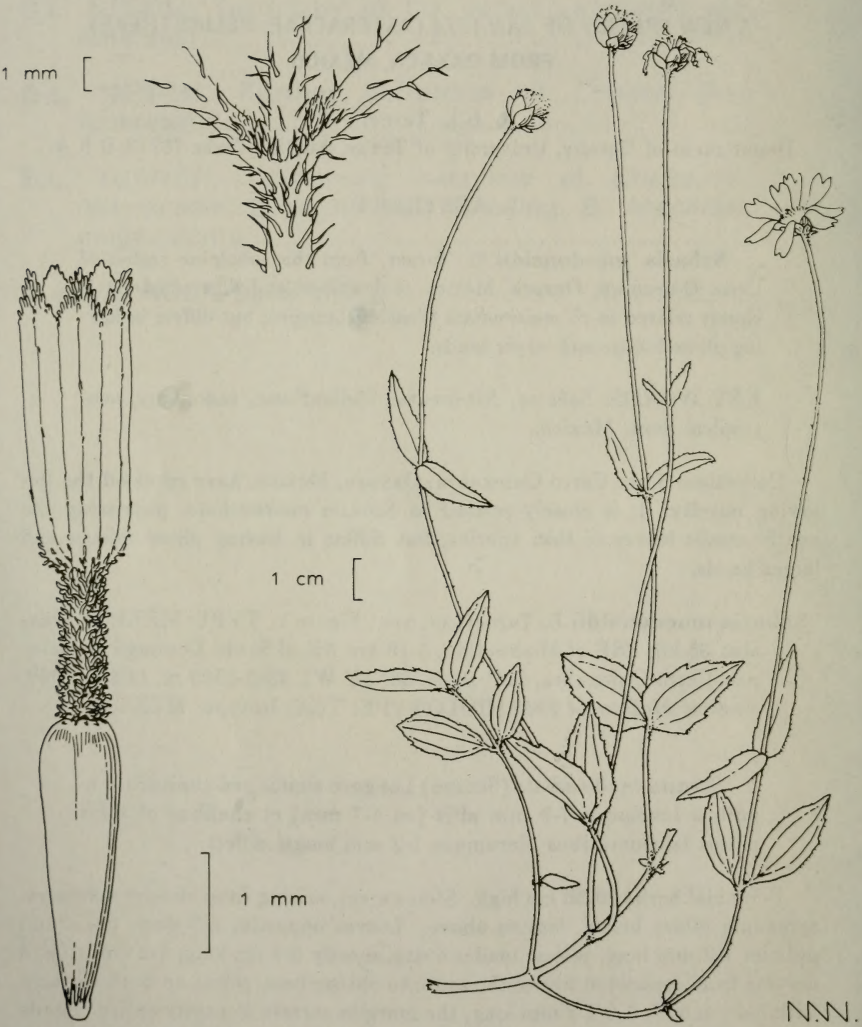


Fig. 1. Sabazia macdonaldii, from holotype.

7-9 nervate beneath, 2-3 lobed. Disk florets numerous, the corollas yellow, pubescent, ca 4 mm long, the tube ca 1 mm long. Achenes ca 3 mm long, black, striolate, glabrous, all of them epappose.

According to label data, the species is common in a pine tree understory, 3 km from the summit of Quixobra along a dirt road to La Cieneguilla.

ACKNOWLEDGMENTS

I am grateful to Dr. Guy Nesom for the Latin diagnosis and to both him and Dr. Linda Escobar for a review of the manuscript. Ms. Nancy Webber provided the illustration.

AN OVERVIEW OF THE *BRICKELLIA LEMMONII* (ASTERACEAE:
EUPATORIEAE) COMPLEX (INCLUDING *B. CONDUPLICATA*)

B.L. Turner

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

The *Brickellia lemmonii* complex (including *B. conduplicata*) of México is treated taxonomically. Four regional intergrading varieties are recognized within this complex: var. **carmenensis** B. Turner, largely restricted to the Sierra Del Carmen of north central Coahuila; var. **conduplicata** (B.L. Robins.) B. Turner, mostly restricted to the middle montane regions of southern Nuevo León and adjacent San Luis Potosí; var. **nelsonii** (B.L. Robins.) B. Turner, mostly restricted to central Nuevo León and adjacent Tamaulipas; and var. *lemmonii*, largely restricted to Chihuahua and adjacent U.S.A. Brief descriptions, a key to the taxa concerned and a map showing distributions are provided.

KEY WORDS: *Brickellia*, Asteraceae, Eupatorieae, México.

Brickellia conduplicata was originally described as a variety of *B. betoniifolia* A. Gray. Robinson (1917) subsequently elevated this to specific rank. It is typified by material from San Luis Potosí, but Robinson confounded its taxonomic status by including elements of this taxon from southern Coahuila within the closely related and earlier *B. cylindracea* Gray & Engelmann. In my forthcoming treatment of *Brickellia* for the Mexican Eupatorieae, I restrict *B. cylindracea* to central Texas and include all of the Mexican elements, along with those from trans-Pecos Texas and adjacent New Mexico, in an expanded *B. lemmonii*. The latter complex is exceedingly variable and has proven to be one of the more difficult groups to treat taxonomically, as noted in the treatment that follows.

Brickellia lemmonii A. Gray, Proc. Amer. Acad. Arts 17:206. 1882.

Robinson (1917) treated *Brickellia lemmonii* as composed of two infraspecific taxa: var. *lemmonii*, which was distinguished by its paniculately branched capitulescence; and var. *wootonii* with a raceme like, mostly unbranched capitulescence. After examination of a broad range of material from México and adjacent U.S.A., I am unable to distinguish between the varieties, the character

of the capitulescence being largely determined by leaf arrangement, opposite leaves producing a panicle like capitulescence, alternate leaves producing a raceme like capitulescence, much as shown in Robinson's (1917) delineation of these taxa. Indeed, the holotype of *B. lemmonii* (GH!) consists of two sprigs, one with alternate leaves, the other with opposite leaves. The sprigs appear to be from different plants, but in nearly all other characters, they are essentially identical. Further, *B. lemmonii* appears to grade into *B. nelsonii* B.L. Robins. in Coahuila México, the latter, in turn, grading into *B. conduplicata* B.L. Robins., as might be inferred from Figure 1. In addition, a fourth infraspecific taxon, var. *carmenensis* B. Turner, is newly described herein. In summary, *B. lemmonii* appears to be a widespread, highly variable species comprised of four intergrading varieties indicated in the treatment that follows.

Key to varieties

1. Blades of leaves ovate, mostly 2-3 times as long as wide; inner involucre bracts mostly acute (2)
- 1' Blades of leaves broadly ovate to subdeltoid, 1-2 times as long as broad; petioles mostly 3-10 mm long; inner involucre bracts obtuse to somewhat rounded (except in var. *carmenensis*) (3)
2. Blades of leaf pallid green, the undersurfaces and stems densely puberulent, the veins raised, reticulate; n Chihuahua, nw Coahuila adjacent U.S.A. var. *lemmonii*
- 2' Blades of leaf not pallid green, the undersurfaces moderately hispid to puberulous along the veins; Coahuila, Nuevo León, Tamaulipas, San Luis Potosí var. *nelsonii*
3. Inner involucre bracts mostly lanceolate with obtuse apices; se Coahuila, Nuevo León, Tamaulipas, San Luis Potosí var. *conduplicata*
- 3' Inner involucre bracts linear-lanceolate with sharply acute apices; Sierra del Carmen, Coahuila var. *carmenensis*

***Brickellia lemmonii* A. Gray var. *carmenensis* B. Turner, var. nov. TYPE:** MÉXICO. Coahuila: W slope of Sierra del Jardín (29° 03' N, 102° 38' W), 1400-2500 m, 16 Sep 1972, *F. Chiang, T. Wendt & M.C. Johnston 9324* (HOLOTYPE: LL; Isotype MEXU).

Brickellia conduplicatae B.L. Robins. similis sed foliis chloroleucis tenuioribus, flosculis numerosioribus, et bracteis involucri acute acutis differt.

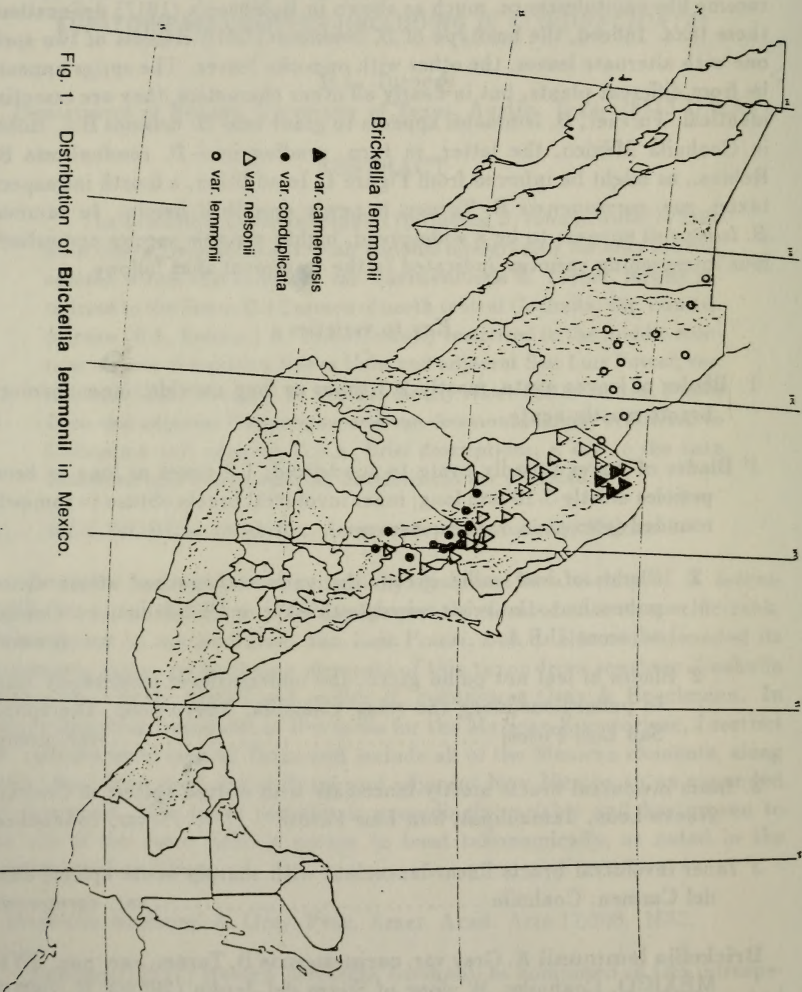


Fig. 1. Distribution of *Brickellia lemmonii* in Mexico.

ADDITIONAL COLLECTIONS EXAMINED: MÉXICO. Coahuila: Sierra Del Carmen, 20 Aug 1936, *Marsh 572* (TEX); Madera Canyon, E side of Sierra Carmen Madera, 22 Aug 1966, *Powell, et al. 1453* (LL,TEX); same locality and date, *Powell, et al. 1466* (LL,TEX).

***Brickellia lemmonii* A. Gray var. *conduplicata* (B.L. Robins.) B. Turner, *comb. nov.* BASIONYM: *Brickellia conduplicata* B.L. Robins., Mem. Gray Herb. 1:79. 1917.**

Suffruticose perennial herbs 30-100 cm high; leaves mostly alternate along the upper stems, 2-4 cm long, 1-3 cm wide; petioles 2-8 mm long; blades broadly ovate, obtuse or rounded at the base, coarsely reticulate veined beneath, moderately strigopuberulent, especially along the veins, the margins crenulodentate; heads usually numerous in both terminal and axillary racemes, the ultimate peduncles mostly 0.5-2.0 mm long; involucre 8-11(-13) mm high, the inner bracts usually purplish, obtuse to rounded at the apices; florets mostly 10-12 per head; achenes 3.5-4.0 mm long, pubescent throughout, the pappus of ca 40 bristles 8-10 mm long. This variety occupies the higher pine-oak zones in the mountains about Saltillo, Coahuila and extends southward in similar habitats to San Luis Potosí. It appears to grade into var. *nelsonii* northward and downslope.

***Brickellia lemmonii* A. Gray var. *nelsonii* (B.L. Robins.) B. Turner, *comb. nov.* BASIONYM: *Brickellia nelsonii* B.L. Robins., Mem. Gray Herb. 1:29. 1917.**

This variety much resembles var. *conduplicata* but the leaves are nearly always ovate to narrowly ovate, 2.5-4.0 times as long as wide, usually acutely tapering upon the blades, the venation less pronounced beneath and heads usually fewer on longer ultimate peduncles (mostly 1-4 cm long vs 0.5-2.0 cm). The taxon is relatively uniform throughout most of Coahuila, but in the area of Saltillo and Monterrey it appears to intergrade upslope with var. *conduplicata*, the type itself appearing to have at least a few characters of the latter taxon.

Brickellia lemmonii A. Gray var. *lemmonii*. *Coleosanthus lemmonii* (A. Gray) Ktze., Rev. Gen. 1:328. 1891.

Coleosanthus wootonii Greene, Bull. Torrey Bot. Club 24:511. 1897.

Brickellia lemmonii A. Gray var. *wootonii* (Greene) B.L. Robins., Mem. Gray Herb. 1:50. 1917.

Coleosanthus densus Greene, Pittonia 4:126. 1900.

Brickellia viejensis Flyr, Sida 3:253. 1968.

This variety much resembles var. *conduplicata* but the leaves are mostly ovate (2.5-3.5 times longer than wide), pallid green, the petioles mostly 0-3 mm long, and the involucral bracts lance-ovate and sharply acute; chromosome number, $n=9$ pairs.

The taxon intergrades southward into var. *nelsonii*, the latter differing in having mostly sparsely hispidulous leaves with longer petioles.

As indicated in Figure 1, var. *lemmonii* occurs in Chihuahua and north-eastern Coahuila, extending northward into trans-Pecos Texas and adjacent New Mexico.

ACKNOWLEDGMENTS

I am grateful to Dr. Guy Nesom for the Latin diagnosis and to both him and Dr. A. McDonald for reviewing the manuscript.

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NEW SPECIES, NAMES AND COMBINATIONS IN MEXICAN ASTERACEAE

B.L. Turner

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

In connection with the preparation of a treatment of the Asteraceae of México, the following new species, names and combinations are proposed: *Ageratina macdonaldii* B. Turner, *Artemisia campestris* L. var. *caudata* (Michaux) B. Turner, *Crepis runcinata* Torrey & Gray var. *barberi* (Greenm.) B. Turner, *Dyssodia pulcherrima* (Strother) B. Turner, *Encelia virginensis* A. Nels. var. *actonii* (Elmer) B. Turner, *Eupatorium guerreroanum* (B. Turner) B. Turner, *Eupatorium rzedowskii* (B. Turner) B. Turner, *Eupatorium surutatoanum* B. Turner, *Eupatorium tenejapanum* B. Turner.

KEY WORDS: Asteraceae, México, nomenclature.

Preparation of a treatment of the Asteraceae of México (Turner & Nesom, in prep.) has occasioned description of the following new species, name changes and new combinations.

Ageratina macdonaldii B. Turner, *sp. nov.* TYPE: MÉXICO. Oaxaca: 35 km ESE of Miahuatlán, 5 km NE of Santo Domingo Ozolotepec, Cerro Quiexobra, timberline vegetation in open glades along ridges and in mountain "saddles," 3650-3800 m (16° 10' N, 96° 15' W), 10 Dec 1989, *Andrew McDonald 2916* (HOLOTYPE: TEX; Isotype: MEXU).

Ageratina prunellifolio (H.B.K.) King & H. Robins. *similis* sed foliis fere sessilibus (petioli 1-2 mm vs 8-15 mm longi) et capitulis majoribus en pedunculis longioribus differt.

Perennial herbs 20-50 cm high. Stems densely glandular pubescent above, arising from a fibrous root system, the lower portion producing lateral rhizomes. Leaves opposite throughout or nearly so (the uppermost, much reduced leaves alternate); petioles 1-2 mm long; blades ovate to elliptic-ovate, 2.0-3.5 cm long, 1.5-2.5 cm wide, 3 nervate, sparsely pubescent beneath with crinkly hairs, especially along the venation, the margins crenulate. Heads 1-3 per primary stem, the ultimate peduncles glandular pubescent, 3.0-4.5 cm long.

Involucres 10-12 mm high, 12-20 mm wide, broadly campanulate to hemispheric, the bracts 2 seriate, subequal, hirsutulous below, the apices acute. Receptacle convex, ca 5 mm across, epaleate, glabrous. Florets numerous, the corollas white, 5.0-5.5 mm long, the tube ca 2 mm long, the throat ca 3 mm long, the lobes ca 0.5 mm long, pubescent with multiseptate trichomes. Achenes fusiform, ca 3 mm long, hispidulous, the pappus of 15-20 fragile white or rosy barbellate bristles ca 5 mm long.

The species is clearly related to the widespread subalpine *Ageratina prunellifolia* but is readily distinguished by its nearly sessile leaves (petioles 1-2 mm long vs 8-15 mm), much longer, glandular pubescent peduncles and larger heads with more numerous florets.

It's a pleasure to name this taxon for its only known collector, Dr. Andrew McDonald, avid student of the alpine flora of México, currently affiliated with the University of Texas, Austin.

Artemisia campestris L. var. **caudata** (Michaux) B. Turner, *comb. nov.*

BASIONYM: *Artemisia caudata* Michaux, *Fl. Bor. Amer.* 2:129. 1803.

This taxon was treated as a subspecies by Hall & Clements (1923). The automatic varietal name, var. *caudata*, was validated by the description of *Artemisia caudata* var. *calvescens* Lundell, *Amer. Midl. Naturalist* 2:188. 1912.

Crepis runcinata Torrey & Gray var. **barberi** (Greenm.) B. Turner, *comb.*

nov. BASIONYM: *Crepis barberi* Greenm., *Proc. Amer. Acad. Arts* 40:52. 1904.

This taxon was treated as a subsp. of *Crepis runcinata* by Babcock (1947). It is typified by material from Colonia García, Chihuahua, México, but also occurs in adjacent New Mexico, U.S.A.

Dyssodia pulcherrima (Strother) B. Turner, *comb. nov.* BASIONYM:

Dyssodia neomexicana (A. Gray) B.L. Robins. var. *pulcherrima* Strother, *Univ. Calif. Publ. Bot.* 48:43. 1969.

This taxon is closely related to *Dyssodia neomexicana* of northeastern Coahuila, but distinguished by a combination of features including smaller heads, shorter involucres (5-7 mm high vs 7-9 mm high), larger ligules (6-8 mm long vs 1-2 mm), larger disk corollas (5-6 mm long vs 3.5-5.0 mm), shorter, white, pappus scales (3.5-5.0 mm long vs tawny and 5-7 mm long) and smaller, less silky pubescent achenes.

Dyssodia pulcherrima was treated by Strother (1969) as varietally distinct from *D. neomexicana*, in spite of a suite of characters and a distribution that suggests that two species are involved. Intergrades do not exist and the two taxa appear as distinct as many another species pair retained by Strother (e.g. *D. littoralis* and *D. anthemidifolia*; *D. aurantia* and *D. appendiculata*, etc.).

Encelia virginensis A. Nels. var. ***actonii*** (Elmer) B. Turner, *comb. nov.*
BASIONYM: *Encelia actonii* Elmer, Bot. Gaz. (Crawfordsville) 39:47.
1905.

Blake (1913) treated this taxon as a variety of *Encelia frutescens*. Keck (1958) treated it as a subspecies of *E. virginensis*, a position to which I also subscribe, but I would opt for the varietal designation, this being the preferred nomenclature for regional variants of a populational nature, the category subspecies, like that of subgenus, to be used when clustering varieties or to indicate the magnitude of divergence, when but a single variety is included within a given subspecies.

Eupatorium tenejapanum B. Turner, *nom. nov.* Based upon: *Bartlettina breedlovei* King & H. Robins., Phytologia 28:286. 1974. \equiv *Eupatorium breedlovei* (King & H. Robins.) B. Turner, Phytologia 67:112. 1989. Not *Eupatorium breedlovei* (King & H. Robins.) B. Turner, Phytologia 64:13. 1987 \equiv *Chromolaena breedlovei* King & H. Robins., Phytologia 47:233. 1980.

In my recent transfer of this species I overlooked the fact that I had already made the combination *Eupatorium breedlovei* in my earlier transfer of *Bartlettina breedlovei* into *Eupatorium*, an inexplicable lapse. The new name proposed here refers to the village of Tenejapa, Chiapas, about which the species distribution is centered.

Eupatorium surutatoanum B. Turner, *nom. nov.* Based upon: *Koanophyllon sinaloensis* B. Turner, Phytologia 63:202. 1987. Not *Eupatorium sinaloense* B.L. Robins., Contr. Gray Herb. 77:39. 1926.

The specific name refers to the mountain range on which the type was collected, Sierra Surutato, Sinaloa.

Eupatorium rzedowskii (B. Turner) B. Turner, *comb. nov.* BASIONYM: *Koanophyllon rzedowskii* B. Turner, Phytologia 63:203. 1987.

Eupatorium guerreroanum (B. Turner) B. Turner, *comb. nov.* BASIONYM: *Koanophyllon guerreroana* B. Turner, Phytologia 63:203. 1987.

ACKNOWLEDGMENTS

I am grateful to Dr. Guy Nesom for the Latin diagnosis and to him and Dr. Linda Escobar for reviewing the manuscript.

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A NEW NAME COMBINATION IN *LEWISIA* (PORTULACACEAE)

Lauramay T. Dempster

Jepson Herbarium, University of California, Berkeley, California 94720 U.S.A.

ABSTRACT

The nomenclature and possible relationships of *Lewisia pygmaea*, *L. nevadensis* and *L. glandulosa* are discussed.

KEY WORDS: *Lewisia*, Portulacaceae, systematics.

Study of the *Lewisia pygmaea* complex has resulted in the following reflections: *Calandrinia pygmaea* Gray and *Calandrinia nevadensis* Gray were published in 1873, with the former having page priority. These were subsequently placed in *Lewisia* by Robinson in 1897. *Oreobroma glandulosum* Rydberg was published in 1932, and subsequently placed in *Lewisia* as a subspecies of *L. pygmaea* by Ferris in 1944. *Lewisia nevadensis* was relegated to the status of subspecies under *L. pygmaea* by Fosberg in 1942. I believe that the chronological order in which these three species were published has had an unfortunate effect on their subsequent taxonomic treatment.

Since it is evident to anyone who has worked on the group that *Lewisia pygmaea* blends on the one hand with *L. nevadensis* and on the other with *Oreobroma glandulosum*, the tendency has been to make the two extremes infraspecific taxa under *L. pygmaea*, the tacit assumption being that the variable and widespread *L. pygmaea* is the parent of the other two taxa. It seems clear to me, however, that this is the wrong approach. *Lewisia nevadensis* and *O. glandulosum* are completely distinct and clearly different from each other. It is only the existence of *L. pygmaea* that blurs that distinction.

There are two possible taxonomic solutions to this problem: 1) to lump all of these plants under one name (i.e. *Lewisia pygmaea*) or 2) to recognize three species, two of which can be clearly defined, at least in relation to each other, the third, however, (*L. pygmaea*) being intermediate, widespread, variable and ill defined.

Contrary to the tacit assumption mentioned above, my theory is that *Lewisia pygmaea* is of hybrid origin, and is continually undergoing introgression from the other two species, although much further work would be needed, particularly with chromosomes and artificial crossing, to verify this. As a result of this supposition, however, the following nomenclature becomes appropriate:

Lewisia pygmaea (A. Gray) B.L. Robinson, in A. Gray, *Syn. Fl. N. Amer.* 1(1):268. Cambridge, 1897. BASIONYM: *Calandrinia pygmaea* A. Gray, *Proc. Amer. Acad. Arts* 8:623. 1873.

Lewisia nevadensis (A. Gray) B.L. Robinson, in A. Gray, *Syn. Fl. N. Amer.* 1(1):268. Cambridge 1897. BASIONYM: *Calandrinia nevadensis* A. Gray, *Proc. Amer. Acad. Arts* 8:623. 1873. *Oreobroma nevadensis* (A. Gray) Howell, *Erythea* 1:33. 1893. *Lewisia pygmaea* (A. Gray) B.L. Robins. var. *nevadensis* (A. Gray) Fosberg, *Amer. Midl. Naturalist* 27:256. 1942.

Lewisia glandulosa (Rydb.) Dempster, *comb. nov.* BASIONYM: *Oreobroma glandulosa* Rydb., in *North American Flora* part 4:325. New York, 1932. *Lewisia pygmaea* (A. Gray) B.L. Robins. subsp. *glandulosa* (Rydb.) Ferris, in *Abrams Illustrated Flora of the Pacific States* II:134. Stanford, 1944.

Morphological discussion and key to species will appear in the forthcoming revision of W.L. Jepson's Manual (Jepson, *Man. Fl. Pls. Calif.* [1925]) to be published in 1993.

ADDENDUM TO AN ANNOTATED CATALOGUE OF TYPE SPECIMENS IN THE UNIVERSITY OF ILLINOIS HERBARIUM (ILL) – PIPERACEAE

Almut G. Jones

Department of Plant Biology, University of Illinois, 505 S. Goodwin, Urbana,
Illinois 61801 U.S.A.

ABSTRACT

Ten names in the Piperaceae are listed for which type specimens (one holotype, 10 isotypes and 1 paratype) are located at ILL. The material was not available in 1985 and 1986, when the two parts of an annotated catalogue of type specimens for members of this family in the University of Illinois herbarium were prepared for publication.

KEY WORDS: Piperaceae, type specimens.

INTRODUCTION

During preparation of the annotated catalogue of type specimens of Piperaceae at the University of Illinois Herbarium (Jones 1985; 1986), one holotype and several isotypes, cited by Standley (1936), Trelease (1936; 1937; 1941) and Yuncker (1957) as being on deposit at ILL, were not found. In our correspondence files of 1951, I found a handwritten note by Dr. Yuncker stating that he "borrowed two bundles of Piperaceae for study." Evidently, the material was hand carried to DPU on the occasion of one of his visits to the Urbana campus. In a letter announcing return of some borrowed material, written in June of 1959 to G.N. Jones, curator at ILL at that time, Dr. Yuncker mentioned that he would retain some specimens about which he still had questions. The material in question, however, was never returned. When inquiring at De Pauw University in Greencastle, IN, I was informed that the Truman G. Yuncker Herbarium was no longer active and was about to be transferred to some other institution. My request for return of the material that belonged to ILL elicited no response. Upon learning that the Yuncker Herbarium had been purchased by the New York Botanical Garden, I told Dr. Patricia K. Holmgren, Director of the Herbarium (NY), about our predicament at ILL, and she promised to be on the lookout for our specimens. To my relief and delight, 26 sheets marked as belonging to ILL were found soon after, and returned to their proper home in September of 1988. The type specimens included in that shipment are listed in the following paragraphs. The format of citation is essentially the same as that used before (Jones 1985; 1986).

Peperomia

cainarachiana Yuncker, Svensk Bot. Tidskr. 51:540. 1957. TYPE: PERÚ. San Martín: Pongo de Cainarachi, Río Cainarachi, tributary of Río Huallaga, El. about 230 m, Sep-Oct 1932, *Klug 2653* (HOLOTYPE: S; Isotype: ILL).

storkii Trel., in Standley, Field Mus. Publ. Bot. 18 (No. 391):326. 1937. TYPE: COSTA RICA. Cerro de La Carpintera, El. 1710 m, 7 Mar 1928, *Stork 1171* (HOLOTYPE: ILL).-[≡ *P. angularis* C.DC. in DC. (fide Wm. Burger, 1970)].

subflaccida Yuncker, Svensk Bot. Tidskr. 51:539. 1957. TYPE: PERÚ. Loreto: Pumayacu, between Balsapuerto and Moyobamba, El. 600-1200 m, Aug-Sep 1933, *Klug 3209* (HOLOTYPE: S; Isotype: ILL).

Piper

baezense Trel., Ciencia (México) 2:207. 1941. TYPE: ECUADOR. Napo-Pastaza, Baeza, *Isern 1753* (HOLOTYPE: MA; Isotype: ILL).-[This species recognized by Trelease & Yuncker, 1950].

cahuapanasense Trel., in Macbr., Field Mus. Publ. Bot. 13 (No. 357):142. 1936. TYPE: PERÚ. Junín: Cahuapanas, on Río Pichis, El. about 340 m, 20-21 Jul 1929, *Killip & Smith 26791* (HOLOTYPE: US; Isotype: ILL).

externum Trel., Ciencia (México) 2:207. 1941. TYPE: PERÚ. Chanchamayo *Isern 2904* (HOLOTYPE: MA; Isotype: ILL).

klugii Yuncker, Svensk Bot. Tidskr. 51:529. 1957. TYPE: PERÚ, San Martín: Zepelacio, near Moyobamba, El. 1200-1600 m, Jan 1934, *Klug 3512* (HOLOTYPE: S; Isotype: ILL).

lundellii Trel. ex Standley, in Standley & Record, Field Mus. Publ. Bot. 12 (No. 350):408. 1936. TYPE: BRITISH HONDURAS (BELIZE). Honey Camp, coastal region, 29 Oct, *Lundell 570* (HOLOTYPE: F 604418; Isotypes (2 sheets): ILL).-[≡ *P. amalago* L. (fide M.C. Tebbs, 1985)].

multimammosum Trel., in Macbr., Field Mus. Publ. Bot. 13 (No. 357):195. 1936. TYPE: PERÚ. Junín: Puerto Bermúdez, El. about 375 m, 14-17 Jul 1929, *Killip & Smith 26645* (HOLOTYPE: US; Isotype: ILL; Paratype at ILL: PERÚ. Loreto: Santa Rosa, lower Río Huallaga below Yurimaguas, El. about 135 m, 1-5 Sep 1929, *Killip & Smith 28848*).

- pygmaeum* Yuncker, Svensk Bot. Tidskr. 51:530. 1957. TYPE: PERÚ. Loreto: Pumayacu, between Balsapuerto and Moyobamba, El. 600-1200 m, Aug-Sep 1933, *Klug 3177* (HOLOTYPE: S; isotype: ILL).

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REINSTATEMENT OF *TONESTUS* (ASTERACEAE: ASTEREEAE)

Guy L. Nesom & David R. Morgan

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

In order to provide a complete, formal nomenclature for the genus *Tonestus*, we propose the following new combinations: *T. aberrans* (A. Nels.) Nesom & Morgan, *T. alpinus* (L. Anderson & S. Goodrich) Nesom & Morgan, *T. graniticus* (Tiehm & Shultz) Nesom & Morgan, *T. microcephalus* (Cronq.) Nesom & Morgan and *T. peirsonii* (Keck) Nesom & Morgan. A generic description of *Tonestus* is presented, and the distinction between *Tonestus* and *Stenotus* is considered. With one exception and one qualification, the nomenclatural combinations in *Tonestus* also complete the apportionment of species of the polyphyletic North American *Haplopappus* (sensu Hall), among its constituent genera.

KEY WORDS: *Haplopappus*, *Tonestus*, Asteraceae, Astereae, North America.

In North America, the genus *Haplopappus* has encompassed a wide variety of species groups (Hall 1928), increasingly recognized in modern literature as phylogenetically disparate (Lane, *et al.* 1987). Although it is perhaps not universally agreed upon, we agree with Brown & Clark (1982) that *Haplopappus* sensu stricto is restricted to several sections that are endemic to South America. *Haplopappus* sect. *Polyphylla* of South America and the genus *Hazardia* of North America are closely similar and they may be congeneric. Except for *Hazardia*, however, none of the North American sections of *Haplopappus* sensu Hall can be considered to be congeneric with true *Haplopappus*.

The following synopsis provides an account of all sections of North American *Haplopappus* and their current taxonomic rank and/or placement. For those wishing to recognize the segregates of *Haplopappus*, the combinations are now available for all species involved, with the few exceptions noted below.

Sect. *Blepharodon* as part of *Machaeranthera* (Hartman 1976). Three species (the "phyllocephalus group") of sect. *Blepharodon* sensu Hall were said by Hartman (1976) to represent an undescribed genus. These three have names as *Machaeranthera* as well as *Haplopappus*.

Sects. *Ericameria*, *Stenotopsis*, *Macronema* and *Asiris*. Nesom, *et al.* (submitted) have removed a group of species as a separate, new genus. These are primarily species of the Chihuahuan Desert, formerly recognized as *Ericameria*. Nesom (1990) has expanded the boundaries of true *Ericameria* as a genus to encompass 27 species formerly belonging to *Haplopappus* sects. *Ericameria*, *Macronema*, *Asiris* and *Stenotopsis*, making the genus coordinate in rank and variability with *Chrysothamnus*, although somewhat larger.

Sect. *Hazardia* as a separate genus (Clark 1979).

Sect. *Hesperodoria* as a separate genus (Greene 1906). As observed by Hall (1928), the two species of *Hesperodoria* are very different from each other. The single remaining species of North American *Haplopappus* without a name in a segregate genus, *Haplopappus salicinus* S.F. Blake, was based on a specimen cited by Hall as *Haplopappus* (*Hesperodoria*) *scopulorum* (M.E. Jones) H.M. Hall. This taxon apparently is still known only from the type collection, and we are not able to make a judgment on its taxonomic placement. Anderson & Weberg (1974) have suggested that it is similar to the monotypic genus *Vanceleva*.

Sect. *Isocoma* as a separate genus (Johnston 1970; Turner 1972; Nesom, in prep.).

Sect. *Isopappus* as the separate genus *Croptilon* (Smith 1965; 1981). One species, *Haplopappus occidentalis* H.M. Hall, has been segregated as the monotypic genus *Benitoa* (Keck 1956).

Sect. *Oonopsis* as a separate genus (Greene 1896).

Sect. *Oreochrysum* as a separate, monotypic genus (Rydberg 1906). Anderson & Creech (1975) have treated it as a species of *Solidago*.

Sect. *Osbertia* as a separate genus (Turner & Sundberg 1986).

Sect. *Prionopsis* as a separate genus (Nuttall 1841; Johnston 1970; Howe 1975).

Sect. *Pyrrocoma* as a separate genus (Mayes 1976).

Sect. *Stenotus* as a separate genus of six species. Greene (1894) reinstated *Stenotus* as a genus, but it has not had a modern treatment at that rank, although that of Hall (1928) remains correct in its essence. Aven Nelson added many taxa that were synonymized by Hall, but only a single additional species has been recognized since Hall's treatment (Nesom 1989).

After the consolidation of *Ericameria*, and with the recognition as genera of the other groups as noted above, 7 North American species remain to be dealt with in *Haplopappus*, all of which are in sect. *Tonestus*. *Tonestus* also has been regarded as a distinct genus (Nelson 1904), and except for the unusual *H. microcephalus*, there appears to be recent general agreement on the members that are included (Anderson 1980; Tiehm & Shultz 1985).

Tonestus is similar to *Stenotus* in its herbaceous habit, primarily monocephalous stems and base chromosome number of $x=9$. The overlapping nomenclatural synonyms demonstrate at least an early lack of understanding

of their relationships and the boundaries between them. Referring primarily to habit, Hall (1928: p. 39) made the claim that "The sections *Stenotus*, *Tonestus*, and *Macronema* form an almost continuous series," and he also placed *Oreochrysum* as a closely related element of this group. More recently, Clark, *et al.* (1980) also referred to *Stenotus* as a "woody shrub," and on the basis of similar habit and flavonoids, placed it in the same lineage as *Macronema* and *Ericameria*. Hall believed that *Stenotus* was phylogenetically connected to *Macronema* as well as *Tonestus*, but Clark, *et al.* (1980) apparently excluded *Tonestus* from a close relationship with the other two. Finally, Nesom (1989) speculated that *Tonestus* might be closely related to *Macronema* and *Stenotus*.

We observe that plants of both *Stenotus* and *Tonestus* are very different from those of the woody shrubs found in *Macronema* and *Ericameria*. The former two have woody roots and caudex branches or rhizomes, the above ground parts are distinctly herbaceous and the basal leaves are persistent. Further, studies of restriction site variation in chloroplast DNA (Morgan, unpubl.) show *Tonestus* (*T. pygmaeus*) to be in the same clade as *Solidago* (*S. altissima* L.), and *Oreochrysum* (\equiv *S. parryi*), most closely related to the latter and very strongly separated from the group of species that includes *Ericameria* (sensu Nesom 1990, including *Macronema*) and *Chrysothamnus*.

Stenotus was not included in Morgan's investigations of DNA restriction sites, but we do not believe that it is necessarily closely related to *Tonestus*. They appear to be distinct, unconnected groups. There are patterns of variability in each genus that are at least superficially similar, but the two can be distinguished morphologically by the features in the following key.

1. Leaves and stems eglandular (short stipitate glandular in 2 species); leaves entire, 3 nerved or when linear, 1 nerved, the cauline absent or reduced to small bracts, not clasping; heads 1 per stem; phyllaries lanceolate to obovate, strongly differentiated from the leaves, not foliaceous, with 3-5 parallel nerves *Stenotus*
- 1' Leaves and stems densely long stipitate glandular (eglandular in 1 species); leaves coarsely toothed (entire in 2 species), 1 or 3 nerved, the cauline well developed, usually continuing unreduced to immediately below the heads, clasping to subclasping; heads 1(-5) per stem (mostly 5-13 in 2 species); phyllaries lanceolate, the outer 1 nerved, usually foliaceous, grading into the bracteal leaves and into the inner phyllaries . *Tonestus*

The species of *Tonestus* are distinguished from *Stenotus* principally by the presence of well developed cauline leaves, 1 nerved phyllaries and usually prominently foliaceous phyllaries. Five of the species have leaves with toothed margins and almost all have a tendency to produce several headed capitulescences. Two species with entire leaves and monocephalous stems (see below) often are similar in general appearance to some species of *Stenotus*, but we

feel that these similarities reflect convergence rather than homology, because in their distinctive phyllaries, they clearly belong with *Tonestus*. Finally, *Tonestus* and *Stenotus* appear to have distinctive ecological preferences. The species of *Tonestus* mostly occur in alpine zones, where they inhabit rock outcrops, cliffs and talus, although *T. pygmaeus* and *T. lyallii* also are commonly found in rocky or gravelly soil. Two species of *Tonestus*, *T. graniticus* and *T. microcephalus*, occur at lower altitudes. The species of *Stenotus* generally grow below alpine altitudes, characteristically with sagebrush (although sometimes reaching alpine habitats) and they occur mostly in rocky or gravelly soil.

To complete the reinstatement of *Tonestus*, we provide a taxonomic summary of the genus with the necessary nomenclatural transfers. This also completes the apportionment of North American *Haplopappus* sensu Hall among its natural segregate genera, except for the problems noted above with the three species of sect. *Blepharodon* sensu Hall and with *H. salicinus*.

Tonestus A. Nelson, Bot. Gaz. (Crawfordsville) 37:262. 1904. *Haplopappus* sect. *Tonestus* (A. Nelson) H.M. Hall, Carnegie Inst. Washington Publ. 389:34. 1928. Type species: *T. lyallii* (A. Gray) A. Nelson

Herbaceous perennials with branched caudices or stout rhizomes, often from a thick taproot, with stems and leaves densely stipitate glandular, eglandular in 2 species. Leaves usually with at least a few coarse teeth, entire in 3 species, the basal persistent, the cauline little reduced upward, the upper clasping to subclasping or not clasping. Heads mostly campanulate, usually solitary, sometimes 2-5 per stem in a loose corymb or in 2 species 5-15; phyllaries lanceolate, 1 nerved, in 3-4 nearly equal series or 5-7 graduated series, the outer foliaceous, often grading into the upper leaves and into the more chartaceous inner phyllaries (not foliaceous in 2 species); receptacles shallowly convex, naked. Ray flowers present or absent, pistillate, fertile, the corollas yellow, prominent. Disc flowers perfect, fertile, the corollas yellow, tubular, slightly ampliate upward; style branch appendages mostly acute, about equal in length to the stigmatic portions, with collecting appendages with short hairs or merely papillate. Achenes narrowly oblong, compressed or slightly fusiform to subcylindric, densely to sparsely strigose sericeous; pappus of numerous barbellate bristles in a single series. Base chromosome number, $x=9$ (Anderson 1980; Tiehm & Shultz 1985; Spellenberg 1986).

1. *Tonestus aberrans* (A. Nelson) Nesom & Morgan, *comb. nov.* BASIONYM: *Macronema aberrans* A. Nelson, Bot. Gaz. (Crawfordsville) 53:226. 1912. *Haplopappus aberrans* (A. Nelson) H.M. Hall, Carnegie Inst. Washington Publ. 389:185. 1928.
2. *Tonestus alpinus* (L. Anderson & S. Goodrich) Nesom & Morgan, *comb. nov.* BASIONYM: *Haplopappus alpinus* L. Anderson & S. Goodrich, Great Basin Nat. 40:73. 1980.

3. *Tonestus eximius* (H.M. Hall) A. Nelson & Macbr., Bot. Gaz. (Crawfordsville) 65:70. 1918. BASIONYM: *Haplopappus eximius* H.M. Hall, Univ. Calif. Publ. Bot. 6:170. 1915.
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5. *Tonestus lyallii* (A. Gray) A. Nelson, Bot. Gaz. (Crawfordsville) 37:262. 1904. BASIONYM: *Haplopappus lyallii* A. Gray, Proc. Acad. Nat. Sci. Philadelphia 1863:64. 1864. ~~*Tonestus lyallii*~~ (A. Gray) J.T. Howell, Fl. N.W. Amer. 300. 1900. *Stenotus*
6. *Tonestus microcephalus* (Cronq.) Nesom & Morgan, *comb. nov.* BASIONYM: *Haplopappus microcephalus* Cronq., Madroño 11:186. 1951.
7. *Tonestus peirsonii* (Keck) Nesom & Morgan, *comb. nov.* BASIONYM: *Haplopappus eximius* subsp. *peirsonii* Keck, Madroño 5:169. 1940. *Haplopappus peirsonii* (Keck) J.T. Howell, Leaflet. W. Bot. 6:86. 1950.
8. *Tonestus pygmaeus* (Torr. & Gray) A. Nelson, Bot. Gaz. (Crawfordsville) 37:262. 1904. BASIONYM: *Stenotus pygmaeus* Torr. & Gray, Fl. N. Amer. 2:237. 1842. *Haplopappus pygmaeus* (Torr. & Gray) A. Gray, Amer. J. Sci., ser. 2, 33:239. 1862. *Macronema pygmaeum* E. Greene, Erythea 2:73. 1894.

The species of *Tonestus* can be divided into four intergrading morphological groups: (1) *T. aberrans* and *T. graniticus* with toothed leaves and phyllaries in 5-7 graduated series; the latter is unusual in its reduced cauline leaves and numerous, campanulate-turbinate heads lacking prominently foliaceous outer phyllaries; (2) *T. alpinus*, *T. eximius* and *T. peirsonii* with toothed leaves and phyllaries in 3-4 nearly equal series; (3) *T. lyallii* and *T. pygmaeus* with entire leaves and phyllaries in 3-4 nearly equal series; the latter is the only species in the genus with an eglandular vestiture; and (4) *T. microcephalus* with entire leaves, heads in definite corymbs and phyllaries not foliaceous but with prominent, herbaceous apical extensions. In these characteristics, *T. microcephalus* is a somewhat aberrant species in the genus, but in its cliffside habitat, stout caudex branches, densely leafy stems and 1 nerved phyllaries, it is best placed in *Tonestus*. In this light, the herbaceous apical extensions of the involucre bracts should prove to be homologous with the foliaceous outer bracts that are characteristic of most of the rest of the genus. *Tonestus graniticus*, which is more securely placed as a species of *Tonestus*, also has differentiated, non foliaceous bracts and corymboid heads and it also occurs in habitats below alpine zones.

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TAXONOMY OF *ACHYROCLINE* (ASTERACEAE: INULEAE) IN MÉXICO AND CENTRAL AMERICA

Guy L. Nesom

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

Three species of *Achyrocline* occur in México and Central America, *A. deflexa* B.L. Robins. & Greenm., *A. turneri* Nesom and *A. ventosa* Klatt, in contrast to previous studies that have recognized only one. The two more common species are partially sympatric and sharply differentiated, as outlined in a key.

KEY WORDS: *Achyrocline*, Asteraceae, Inuleae, México, Central America.

Achyrocline is similar to *Gnaphalium*, differing primarily by its very small, few flowered, cylindric heads with few series of phyllaries. It is a genus of 25-30 species primarily from South America (Giangualani 1976), tropical Africa and Madagascar.

Three species of *Achyrocline* occur in México and Central America, although one has been recognized in recent treatments. Standley & Steyermark (1940) correctly regarded *A. yunckeri* S.F. Blake as a synonym of *A. deflexa* B.L. Robinson & Greenm., and this treatment was followed in Guatemala by Nash (1976). Blake's observation that two species were present in Central America was correct, but his recognition of *A. yunckeri*, was based on a misperception of the identity of *A. deflexa*. The plants of "*A. deflexa*" that he contrasted with *A. yunckeri* were clearly what I recognize here as a distinctive but previously undescribed species.

Achyrocline (Less.) DC., *Prodr.* 6:219. 1838. Type species: *Achyrocline* (*Gnaphalium*) *satureoides* (Lam.) DC. *Gnaphalium* subg. *Achyrocline* Less., *Synops. Comp.* 332. 1832.

Perennial herbs with tomentose or closely woolly stems and leaves, sometimes glandular. Leaves alternate, sessile, entire, lanceolate to linear lanceolate, often bicolored, decurrent to a winged stem in some species. Heads disciform, heterogamous, fusiform-cylindric, sessile in dense, terminal, glomerules;

phyllaries in 2-4 graduated or equal series, yellow to cream, scarious, usually basally woolly; receptacles flat, usually ebracteate. Pistillate flowers peripheral, 3-6, the corollas filiform-tubular, sometimes with glandular apices; hermaphroditic flowers central, 1-3, with fertile ovaries, the corollas narrowly funnelform-tubular, often with glandular apices. Achenes oblong, glabrous; pappus of separate, basally caducous bristles. Base chromosome number, $x=14$.

KEY TO THE SPECIES

1. Plants 15-20 cm tall; leaves 2-3 cm long, decurrent; hermaphroditic corollas 2.5 mm long *A. ventosa*
- 1' Plants 50-120 cm tall; leaves 4-11 cm long, not decurrent; hermaphroditic corollas 3.0-3.5 mm long (2)
2. Leaves spatulate, the blades ovate-lanceolate, sharply attenuate to a petiolar base, woolly pubescent with hairs filiform to the very base, the surfaces eglandular; mature phyllaries whitish scarious, smoothly rounded to a minute but definite apiculum, eglandular; corollas filiform-tubular, eglandular, abruptly bulbous indurated at the very base *A. deflexa*
- 2' Leaves narrowly elliptic-lanceolate, gradually attenuate to the sessile base, woolly pubescent with hairs arising from vitreous, erect, thick bases, the surface also with scattered, minute, sessile, resin glands; mature phyllaries yellow scarious, slightly lacerate apically, not definitely apiculate, at least the inner gland dotted; corollas apically glandular when young, not basally inflated *A. turneri*

Achyrocline deflexa B.L. Robinson & Greenm., Amer. J. Sci. 50:153. 1895.
TYPE: MÉXICO. Oaxaca: Sierra de San Felipe, 7000-8000 ft, Nov 1894,
C.G. Pringle 6054 (HOLOTYPE: GH; Isotype: F!).

Achyrocline yunckeri S.F. Blake, Field Mus. Nat. Hist., Bot. Ser. 17:399.
1938. TYPE: HONDURAS. Dept. Comayagua: hills above the
plains of Siguatapeque, wet cliff near El Achote, 1350 m, 15 Jul
1936, *T.G. Yuncker, R.F. Dawson & H.R. House 5872* (HOLO-
TYPE: US; Fragment: LL!).

Erect herbs 0.5-1.2 m tall. Leaves spatulate, the blades ovate-lanceolate, 4-8 cm long, 8-17 mm wide, sharply attenuate to a petiolar base, strongly discolorous, woolly pubescent with hairs filiform to the very base, the surfaces eglandular. Phyllaries 8-11, whitish scarious, with apices smoothly rounded to a minute but definite apiculum, eglandular, the innermost with a definite,

narrow, medial, herbaceous patch on the lower half. Corollas filiform-tubular, eglandular, abruptly bulbous indurated at the very base, pistillate corollas 4-5, 2.5-2.9 mm long, hermaphroditic corollas 1-2, 3.0-3.5 mm long, the lobes with minute, white, clavate hairs, eglandular.

México (Oaxaca, and probably adjacent Chiapas), Guatemala, Honduras, Nicaragua; moist, mixed woods, pine or pine-oak woods, less commonly in cloud forests; 900-2400 m; November-June.

Representative collections examined: GUATEMALA. Dept. Chimaltenango: Barranco de La Sierra, SE of Patzum, 31 Dec 1938, *Standley 61612* (F). Dept. El Progreso: between El Jute de Cobana and Finca Piamonte, 3 Feb 1942, *Steyermark 43365* (F). Dept. Huehuetenango: near crossing of Río San Juan Ixtlan, E of San Rafael Petzal, 9 Jan 1941, *Standley 83014* (F). Dept. Guatemala: 10 km S of San Raimundo, 18 Jan 1939, *Standley 62903* (F). Dept. Jalapa: mountains along the road between Jalapa and Paraiso, 14 Nov 1940, *Standley 77369* (F). Dept. Quezaltenango: Volcán Santa María, between Santa María de Jesus, Los Mojadas, and summit of volcano, 12 Jan 1940, *Steyermark 33918* (F). Dept. Quiché: forested barranca S of Chichicastenango, 11 Jan 1939, *Standley 62411* (F). Dept. Zacapa: upper slopes, along Río Repollal to summit of mountain, 12-13 Jan 1942, *Steyermark 42509* (F).

HONDURAS. Dept. Cortes: Montaña San Idalfonso entre Banaderos y Cusuco, bosque mixto y lluvioso, 1400 m, 26 Mar 1963, *Molina R. 11443* (F,LL). Dept. El Paraiso: along Manzaragua Road, 5 Jan 1947, *Williams & Molina 11505* (F). Dept. Morazan: Quebrada Valle Angeles, 1 km NE de Valle de Angeles, 12 Mar 1963, *Molina R. 11298* (F); slopes of Cerro de Uyuca, along trail between Hoya Grande and Valle Encantado, 2 Dec 1948, *Standley 15302* (F). Dept. Ocotepeque: along Agua Caliente river, vicinity of Honduras-Guatemala border, 25 Jan 1976, *Molina R. 31437* (F).

NICARAGUA. Dept. Jinotega: SE of Jinotega, along road to La Cantera and Los Pinos, 25 Jun 1947, *Standley 10131* (F). Dept. Matagalpa: Jinotega rock quarry, ca 5 km NW of Sta. Maria de Ostuma, 18 Jan 1965, *Williams, et al. 27955* (F).

Achyrocline turneri Nesom, *sp. nov.* TYPE: GUATEMALA. Dept. Baja Verapaz: Unión Barrios, in high forest on hill, 12 Mar 1972, *Contreras 11271* (HOLOTYPE: LL; Isotype: LL).

Achyrocline deflexae B.L. Robinson & Greenm. similis sed foliis elliptici-lanceolatis sessilibus, trichomatibus foliorum basibus crassis, phyllariis glandulosis non-apiculatis, corollis glandulosis ad apices differt.

Erect herbs 0.4-1.2 m tall. Leaves narrowly elliptic-lanceolate, 4-11 cm long, 6-14 mm wide, gradually attenuate to the sessile base, woolly pubescent

with hairs arising from vitreous, erect, thick bases, the surface also with scattered, minute, sessile, resin glands, sometimes more easily visible under the dense wool of the lower surface. Phyllaries 9-11, yellow scarious, not definitely apiculate, the inner with a lower-medial, broadly ovate, herbaceous portion with minute, easily deciduous, orange, sessile glands. Corollas filiform-tubular, not basally inflated, the pistillate corollas 4-5, 2.5-3.0 mm long, hermaphroditic corollas 1-2, mostly 3.5 mm long, the lobes sessile glandular at least when young, also with a few minute, white, clavate hairs.

Guatemala, Honduras and Nicaragua; pine-oak or mixed deciduous woods; (1000-)1300-2400 m; November-April.

Additional collections examined: HONDURAS. Dept. Olancho: along Río Olancho, on road between San Francisco de la Paz and Gualaco, 13.6 mi SW of Gualaco, in disturbed virgin forest on steep slope ca 1/2 mi E of main road, 1300 m, 6 Feb 1987, *Croat & Hannon 64237* (TEX). Dept. Morazan: Cerro de Uyuca, trail between Las Flores and La Labranza, 7 Apr 1949, *Standley 18924* (F).

NICARAGUA. Dept. Matagalpa: Camino al Sanatorio de Aranjuez, 21 Feb 1980, *Araquistain & Sandino 1426* (F); Fuente Pura, km 144 carretera a Jinotega, 20 Feb 1981, *Moreno 7073* (F).

Achyrocline turneri is named for Dr. B.L. Turner, whose initial curation of Mexican and Central American Inuleae has been of invaluable help in further studies, including this one. The species is less commonly collected and apparently not quite as widespread as *A. deflexa*. The two, however, are sympatric and have been collected in close proximity to one another. No intermediates have been observed.

Achyrocline ventosa Klatt, *Linnaea* 42:112. 1878. TYPE: MÉXICO. Locality not specified, but probably Hidalgo or Querétaro, no date, *Ehrenberg 577* (GH-fragment and drawings!).

Herbs 15-20 cm tall. Leaves lanceolate, epetiolate, slightly decurrent but apparently not auriculate, 2-3 cm long, 2-4 mm wide, bicolored, white woolly beneath, glabrescent above, the hairs thin based or with a broadened, flattened, vitreous base, the surfaces apparently not glandular. Phyllaries 11, 4.5 mm long, narrowly triangular with an attenuate-apiculate apex, with minute resin glands near the base. Corollas filiform-tubular, basally expanded but not abruptly bulbous, the pistillate flowers 3, with corollas 2 mm long, the hermaphroditic flowers 1, with corollas 2.5 mm long, eglandular but with a few, minute hairs.

Known only from the type collection.

This diminutive species is similar to *Achyrocline turneri* in its lanceolate, epetiolate leaves and glandular phyllaries, but in addition to the features noted in the key, it differs in its leaves without sessile glands and without prominent,

thick based hairs, its eglandular corollas and its phyllary morphology. In its small stature and short corollas, it is similar to *A. ramosissima* Rusby of the high Andean habitats in Bolivia and Perú. The possibility of a close relationship between these should be investigated, but *A. ramosissima* has sessile, nondecurent leaves, broader phyllaries with rounded, obtuse apices and appears to be specifically distinct.

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TAXONOMIC STATUS OF *GAMOCHAETA* (ASTERACEAE: INULEAE) AND THE SPECIES OF THE UNITED STATES

Guy L. Nesom

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

Gamochaeta is maintained as a separate genus apart from *Gnaphalium*. Descriptions, synonymy, general geographic ranges and a key are given for the six species of *Gamochaeta* that occur in the United States: *G. americana* (Miller) Wedd., *G. falcata* (Lam.) Cabrera, *G. pensylvanica* (Willd.) Cabrera, *G. purpurea* (L.) Cabrera, *G. sphacilata* (Kunth) Cabrera and *G. ustulata* (Nutt.) Nesom. The last species has been generally considered to be a synonym of *G. purpurea*, but it is a distinctive endemic of the Pacific coast from California to southwestern British Columbia.

KEY WORDS: *Gamochaeta*, *Gnaphalium*, Inuleae, United States.

The distinctiveness of *Gamochaeta* from *Gnaphalium* has been emphasized recently, primarily by Cabrera (1961 and later floristic treatments of South American species; e.g., 1971; 1978). Cabrera, however, provided almost no discussion to substantiate his taxonomy and in other treatments of the Gnaphaliinae, *Gamochaeta* has been recognized as a subgroup of *Gnaphalium* (Wagenitz 1965; Drury 1971; Hilliard & Burt 1981; but see Holub 1976). The primary comparative morphological study to include *Gamochaeta* has been that of Drury (1970), who found it to be a distinctive group within the species he sampled, although he retained it as a subgroup of *Gnaphalium* within his GROUP I (the "gnaphalioid cudweeds").

In a study of southern African taxa of Gnaphaliinae, primarily emphasizing characters of the phyllary stereome, achenial pubescence and leaf margins, Hilliard & Burt (1981) have suggested that the circumscription of *Gnaphalium* (as typified by *G. uliginosum* L.) be sharply restricted, and most of its species are native to Africa. Although they segregated numerous genera from *Gnaphalium* in Africa, and regard many of the traditional North American taxa as the genus *Pseudognaphalium* Kirpinczn., they tentatively retained *Gamochaeta* within *Gnaphalium*, while acknowledging that the achenial hairs of the two groups appear to be different.

Although *Gamochaeta* may be related to *Gnaphalium* sensu stricto (sensu Hilliard & Burt 1981), the characters that separate it from that group are at least as significant as those used to distinguish other generally accepted, seemingly closely related genera (e.g., those centered around *Filago* and *Psilocarphus*) and those features used to split a number of the small genera recently proposed in southern Africa. Plants of *Gamochaeta* are morphologically distinguished by their combination of small heads in a spiciform capitulescence, few (2-5) hermaphroditic flowers per head, blunt-truncate collecting appendages of the disc flower style branches, monomorphic, eciliate, pappus bristles basally connate in a distinctive manner and achenes with mucilage producing, rounded-conic hairs. In addition, the peculiar and very prominent concavity developed in the post fruiting receptacles, a feature not previously noted as distinctive of the group, appears to be rare elsewhere in the Gnaphaliinae. The generic identity of plants of *Gamochaeta* is immediately recognizable, and there are no species dubiously included or excluded from it.

Plants of *Gnaphalium* sensu stricto have basally caducous bristles and in some species the bristles are partially to wholly connected at the base, but they remain more or less discrete, joined by short, interlocking cilia ("patent" cilia, in the terminology of Hilliard & Burt 1981) originating from near the bristle base. In *Gamochaeta*, the bristles are always completely fused into a basal cylinder of more or less quadrate cells, the individual bristles having no separate identity. The achenial trichomes of *Gnaphalium* are 3 celled, longer than wide though variable in length, and among the species I have examined, variable in their release of mucilage. All species of *Gamochaeta* uniformly have trichomes as wide as long and composed of two even sized cells that always open to release mucilage.

Two species of *Gnaphalium* sensu stricto often produce a spiciform capitulescence: *G. pauciflorum* DC., of South Africa, sometimes with basally fused pappus bristles and *Gnaphalium polycaulon* Pers., a pan-tropical weed with separate pappus bristles (included by Drury 1970, as *G. indicum* L.). In the New World, the latter is sometimes mistakenly identified as *Gamochaeta*, apparently because of its general aspect. According to Hilliard (1981: p. 290), however, even between *G. pauciflorum*, which among the species of *Gnaphalium* sensu stricto appears to be most similar to *Gamochaeta*, the similarities are not homologous. "Both the form of the pappus and the type of basal fusion in *G. pauciflorum* is different from that in sect. *Gamochaeta*; the involucre bracts too are different in form and texture: there is no relationship here."

Despite these constant, but seemingly small differences, the overall resemblance between *Gnaphalium* sensu stricto and *Gamochaeta* is striking. Without an overview of the subtribe, the two might still be treated as congeneric. Based on observations by Dr. Michael Dillon (in prep.) of details of achenial vestiture and pappus, however, the closest relatives of *Gamochaeta* are South American taxa rather than *Gnaphalium*, and *Gamochaeta* should be treated

as a distinct genus. The analysis by Anderberg (1989) also has emphasized the distinctive trichome morphology of *Gamochaeta* in placing it in a lineage separate from that of true *Gnaphalium*.

The observation that *Gamochaeta* is not the sister group of *Gnaphalium* sensu stricto supports the hypothesis of Hilliard & Burt (1981: p. 227) that "there are no taxonomic links across the southern oceans . . . The regional developments of endemic genera with the Gnaphaliinae appear to be quite independent of one another." The coherent geographic distribution of *Gamochaeta* in the New World (natively) is distinctive. *Gnaphalium* sensu stricto primarily comprises a group of species mostly native to Africa. Only a few are native to North and Central America, although several others occur as naturalized weeds.

Omalotheca Cass. is the only other group besides *Gamochaeta* with spiciform capitulescences and basally fused pappus bristles that has sometimes been included in *Gnaphalium*. These plants are primarily Eurasian, boreal-alpine, rhizomatous perennials with very different achenial, floral and phyllary morphology; the resemblance is superficial and they appear to be only remotely related to *Gamochaeta* (Nesom 1990).

Gamochaeta comprises about 25-35 species (Cabrera 1961; but about 80 species, Cabrera 1978), which are mostly restricted in their native range to South America, with only 5-6 apparently native to North America, including México and Central America (Nesom, in prep). There are no autochthonous Old World taxa. A number of the annual species have strongly weedy tendencies and occur outside of their native areas.

The species of *Gamochaeta* are separated by differences primarily in duration, leaf shape, distribution of pubescence, and the morphology of the capitulescence and phyllaries. Small morphological differences between taxa are typical, but the taxa accepted here can usually be identified with little problem, especially if a set of correctly named reference specimens is at hand. The treatment of southeastern United States *Gamochaeta* as a single species (Cronquist 1980) is too conservative; that of Godfrey (1958) is nearly the same as presented here. At the other extreme, Cabrera (1961), whose species concept apparently is extremely narrow, recognized many names that appear to be synonyms. There is no means of identifying South American specimens that are from outside the southeastern part of the continent, and a comprehensive study of the entire genus is badly needed.

Drury (1971) noted that difficulties in the identification of species of *Gamochaeta* are associated with the lack of "strong correlations among their gross structural features." As further summarized by Drury, there is no evidence for apomixis in the genus, but the small, essentially closed heads with few staminate flowers suggest that they may be autogamous. Such a breeding system might account for at least part of the variability and proliferation of names. Another factor contributing to the difficult taxonomy seems to be an overly

typological approach to recognizing species. Closely similar taxa separated chiefly by differences in length or degree of interruptedness of the capitulescence, or by leaf shape or persistence of basal leaves, should be suspected of being conspecific, at least as a null hypothesis. Such features appear to be highly variable among plants within even a small area.

In the course of taxonomic studies of the Mexican and Texan species of *Gnaphalium* *sensu lato*, it became clear that the application of names to North American "gamochaetoid" species has been extremely uneven. The following summarizes my conclusions regarding the species present in the United States and their identities. These also are the most abundant ones in México, although several others occur there sporadically as waifs. Because of the weedy nature of these taxa, they probably can be expected to occur over a wider area than I have documented here, based on specimens from LL and TEX.

The synonymy below includes only names that apply to North American collections. As noted below, the application of some of the names is still equivocal, and a future study of historical type specimens may require readjustment of some of them. This treatment, however, which is based on examination of specimens from all of the United States, México, Central America and the West Indies, should at least provide a firmer basis for evaluating the nomenclature.

Gamochaeta Wedd., *Chl. And.* 1:151. 1855. Type species: *Gamochaeta* (*Gnaphalium*) *americana* (Miller) Wedd. *Gnaphalium* sect. *Gamochaeta* (Wedd.) O. Hoffm., *Nat. Pflanzenfam.* 4, 5:188. 1894. *Gnaphalium* subg. *Gamochaeta* (Wedd.) Gren., *Fl. Ch. Jurass* 427. 1869.

Taprooted or fibrous rooted annuals or perennials, sometimes rhizomatous, with erect to procumbent or decumbent stems, eglandular, at least stems and leaves densely and closely woolly, the leaves often with glabrescent upper surfaces. Leaves linear to spatulate with entire, flat margins, sessile to subclasping. Heads heterogamous, in a continuous or interrupted spicate capitulescence, in few headed individuals, reduced to a compact terminal glomerule; phyllaries graduated in 5-7 series, at least the inner with an undivided and nonfenestrated stereome; sometimes purplish tinted on the apex and margins; receptacles naked, prominently concave at post fruiting. Pistillate flowers fertile, numerous in several series, the corollas filiform-tubular. Hermaphroditic flowers fertile, 2-5, the corollas narrowly tubular with lobes erect or reflexed; collecting appendages of the style branches mostly blunt-truncated. Achenes 0.4-0.9 mm long, the epidermal surfaces smooth, with mucilage producing, rounded-conic hairs as wide as long; pappus monomorphic, of basally fused, eciliate, scabrid bristles basally caducous and released as a unit. A chromosome number of $n=14$ pairs have been reported for some of the species, with several reports of $n=7$ pairs for *G. purpurea*. Until voucher specimens have been examined, however, association of numbers with names should be suspect.

KEY TO THE SPECIES

1. Plants strongly perennial from thick, lateral rhizomes *G. ustulata*
- 1' Plants annual or biennial from a slender taproot or fibrous roots, without rhizomes (2)
 2. Leaves strongly to weakly bicolored with greenish glabrescent upper surfaces, spatulate-obovate to oblanceolate, the basal present or absent at flowering (4)
 - 2' Leaves equally gray-green pubescent above and beneath, not bicolored, linear to narrowly oblanceolate; basal leaves absent at flowering (3)
3. Bracteal leaves of capitulescence arcuate and more or less at right angles to the spike; inner phyllaries with distinctly brown apices, the outer with acuminate-attenuate apices *G. sphacilata*
- 3' Bracteal leaves of capitulescence straight and ascending; phyllaries distinctly brown, the inner with brown tips and the outer often completely brownish, the outer with acute to rounded apices *G. falcata*
 4. Phyllaries completely glabrous, the outermost broadly ovate, usually with an obtuse apex *G. americana*
 - 4' Outer phyllaries densely to lightly woolly at the base, the outermost ovate-triangular, with an acute to acute-acuminate apex (5)
5. Cauline leaves obovate-spatulate, weakly bicolored; capitulescence usually interrupted; outer phyllaries ovate-triangular with acuminate-apiculate apices, the inner 3.0-3.5 mm long, not apiculate; receptacles deeply concave or crateriform *G. pennsylvanica*
- 5' Cauline leaves mostly oblanceolate, strongly bicolored; capitulescence usually continuous; outer phyllaries ovate-triangular with an acute apex; the inner (3.5-)4.0-5.0 mm long, usually with a minute but distinctly keeled apiculum; receptacles concave but not deeply *G. purpurea*

TAXONOMIC SUMMARY

1. *Gamochaeta americana* (Miller) Wedd., *Chlor. And.* 1:151. 1856. BASIONYM: *Gnaphalium americanum* Miller, *Gard. Dict.* ed. 8, *Gnaphalium* no. 17. 1768. TYPE: JAMAICA. "Sloan. Cat. Jam. 125," not seen. Cabrera (1961) cited "Houstoun, 1731" (BM) as the type. *Gnaphalium purpureum* L. var. *americanum* (Miller) Klatt, *Linnaea* 42:140. 1878.

Gnaphalium guatemalense Gandoger, Bull. Soc. Bot. France 65:42. 1918.
TYPE: GUATEMALA, not seen. As synonym *fide* Nash 1976.
Gamochaeta guatemalensis (Gandoger) Cabrera, Bol. Soc. Argent.
Bot. 9:371. 1961.

Gnaphalium spicatum Lam., *Encycl. Method.* 2:757. 1786. TYPE:
URUGUAY, Montevideo, *Commerson s.n.*, not seen. Cabrera (1961)
cited as the type, a specimen from P, "Des environs de Buenos
Aires ... Commerson." Not *G. spicatum* Miller, *Gard. Dict.*, ed.
8, *Gnaphalium* no. 24. 1768, which apparently is *Pterocaulon vir-*
gatum (L.) DC. *Gamochaeta spicata* (Lam.) Cabrera, Bol. Soc.
Argent. Bot. 9:380. 1961. *Gnaphalium purpureum* L. var. *spicatum*
(Lam.) Klatt, *Linnaea* 42:140. 1878; not (Lam.) Baker 1882.

Annuals or biennials. Leaves spatulate to oblanceolate-obovate, often apiculate, distinctly bicolored, the basal often persistent, the cauline continuing into the lower part of the capitulescence. Capitulescence usually dense and continuous, less commonly interrupted, variable in length from 2-20 cm. Phyllaries completely glabrous, shiny, sometimes purple tinged, the outermost ovate with rounded to obtuse or slightly acute apices, ca 1/3-1/2 as long as the inner, the innermost 3.5-4.0 mm long, with distinctly brown hyaline terminal appendages with a rounded to blunt apex. Chromosome number, $n=14$ pairs.

Apparently adventive and uncommon in near coastal localities in the southeastern United States, specimens seen from Texas, Mississippi, Alabama, Florida, Georgia, South Carolina and North Carolina, one from California (Humboldt Co. *Tracy 15057*, TEX), widespread in western to central and southern México, through Central America, West Indies, South America; (January-April-November).

This species is easily recognized by its strongly bicolored leaves and shiny, completely glabrous phyllaries, the outer broadly ovate. *Gamochaeta purpurea* is distinguished from *G. americana* in its inner phyllaries more commonly purple tinged and with translucent to slightly brownish, minutely but distinctly apiculate apices and its ovate-triangular outer phyllaries 1/2-2/3 as long as the inner and with lightly woolly bases.

The couplet provided by Adams (1972) to separate *Gamochaeta americana* and *G. purpurea* in Jamaica, almost certainly referred to *G. americana* (the type from Jamaica) and what is treated here as *G. pensylvanica*. Adams (1972) recognized only two taxa from Jamaica, and I have seen only specimens of *G. americana* and *G. pensylvanica* from that island. The taxon from New Zealand identified by Drury (1971) as *Gnaphalium spicatum* is very clearly what is treated here as *Gamochaeta americana*, as are the illustrations and description of *G. spicata* provided by Cabrera (1971; 1978). The identity of what both Cabrera and Drury have called "*Gnaphalium americanum*" is not clear, although it appears very similar to what is called here *G. purpurea*. Cabrera

apparently has not identified the latter from southeastern South America, but several Brazilian specimens at LL-TEX are identical to *G. purpurea* of the eastern United States; Drury, however, included both *G. purpurea* and "*G. americana*" among the New Zealand adventives.

For whatever reason, should *Gnaphalium spicatum* prove to be a species separate from *G. americanum*, another name for the former will be necessary, because Larmarck's *G. spicatum* is illegitimate as a later homonym, following 18 years after the publication of the same name by P. Miller (see citation above).

2. *Gamochaeta falcata* (Lam.) Cabrera, Bol. Soc. Argent. Bot. 9:370. 1961. BASIONYM: *Gnaphalium falcatum* Lam., *Encycl. Method.* 2:758. 1786. TYPE: URUGUAY. Montevideo, *Commerson s.n.*, not seen. *Gnaphalium purpureum* L. var. (β) *falcatum* (Lam.) Torr. & Gray, *Fl. N. Amer.* 2:428. 1843. *Gnaphalium stachydifolium* Lam. var. *falcatum* (Lam.) Klatt, *Linnaea* 42:140. 1878.

Gnaphalium heteroides Klatt, *Linnaea* 42:137. 1878. TYPE: MÉXICO. Locality unspecified, *Ehrenberg* 972 (GH-fragment and drawings!).

Gnaphalium stagnale I.M. Johnston, *Contr. Gray Herb.*, ser. 2, 68:99. 1923. TYPE: MÉXICO. San Luis Potosí: Marshes about San Luis Potosí, Aug 1876, *Schaffner* 225 (HOLOTYPE: GH!).

Gnaphalium calviceps Fernald, *Rhodora* 37:449. 1935. TYPE: UNITED STATES. Virginia: Princess Anne Co., Cape Henry, The Desert, sandy pinelands, 28-29 Jul 1934, *Fernald & Long* 4245 (HOLOTYPE: GH; Isotype: LL!).

Gnaphalium subfalcatum Cabrera, *Revista Mus. La Plata Bot.*, ser. 2, 4:174. 1941. TYPE: ARGENTINA, not seen. *Gamochaeta subfalcata* (Cabrera) Cabrera, *Bol. Soc. Argent. Bot.* 9:370. 1961.

Annuals. Stems with erect to procumbent, 6-40 cm tall. Leaves equally pubescent above and beneath, not at all bicolored, linear or narrowly lanceolate with the lower often oblanceolate, 2-3 cm long, 2.0-3.5(-5.0) mm wide, the upper commonly but not always folded. Capitulescence continuous, less commonly strongly interrupted, equally leafy from bottom to top or the leaves reduced in length above the middle. Phyllaries lanceolate with narrowly to broadly acute or rounded apices, basally woolly or at least basally submerged in wool of subtending leaves or bracts, sometimes rose tinged, the inner with hyaline apices merely tinged with brown.

Common from southeastern Texas to Florida and north to Virginia along the Atlantic coast, rare and adventive in southern Arizona and California, in México scattered mostly in the northwest, abundant in South America and perhaps native there, also adventive in Europe; commonly in open, sandy

soil, arroyos, river and pond banks, other disturbed habitats; February-July (-August).

Gamochaeta falcata is distinctive in its relatively narrow, gray-green leaves that are equally pubescent above and beneath, usually with the upper sharply folded and in its leafy capitulescence. The degree of variation in leaf shape in a single species in the eastern United States appears to be great enough to account for the small differences said to exist between *G. falcata*, *G. subfalcata* and *G. calviceps*. Cabrera (1961; 1978) has identified plants of both *G. calviceps* and *G. subfalcata* from North America, separated by the degree of thickness and continuousness of the spikes, features I find variable and intergrading. Godfrey (1958) also recognized *G. falcata* and *G. calviceps* as distinct, but primarily on the basis of phyllary pubescence. The leaves are usually linear but vary toward oblanceolate. South American collections of *G. subfalcata* and *G. falcata* from Uruguay also appear to be variable and fall within the range observed for those from North America. It is on this basis that I consider these three taxa conspecific.

Gnaphalium heteroides is tentatively included here as a synonym. Although it is definitely a species of *Gamochaeta*, it is atypical of *G. falcata* in its smaller stature and smaller, more obovate-spatulate leaves. It might represent a depauperate individual of *G. falcata*, or it might be a South American species adventive in México. I have seen no other specimens from México that are a close match to the type specimen from GH.

3. *Gamochaeta pensylvanica* (Willd.) Cabrera, Bol. Soc. Argent. Bot. 9:375. 1961. BASIONYM: *Gnaphalium pensylvanicum* Willd., Enum. Hort. Berol. 867. 1809. TYPE: UNITED STATES. Pennsylvania: not seen.

Gnaphalium spathulatum Lam., Encycl. Method. 2:758. 1786. TYPE: ARGENTINA. Near Buenos Aires, Commerson s.n., not seen; not Burm. f. 1768 or Phil. 1895. *Gnaphalium purpureum* L. var. *spathulatum* (Lam.) Baker in Martius, Fl. Brasil. 6:125. 1882; Not *Gnaphalium purpureum* L. var. *spathulatum* (Lam.) Ahles 1964.

Gnaphalium peregrinum Fernald, Rhodora 45:479. 1943. TYPE: UNITED STATES. Louisiana: Rapides Parish, N edge of Pineville, burnt-over pine-scrub oak sandhills, 30 Jul 1938, D.S. & H.B. Correll 9937 (HOLOTYPE: GH, photo! Rhodora 45:pl. 479. 1943). Proposed by Fernald to replace the later homonym *Gnaphalium spathulatum* Lam.

Annuals. Stems erect to procumbent, 10-50 cm tall. Leaves usually oblanceolate to obovate-spatulate and basally narrowed to a petiolar region, often apiculate and with closely sinuate margins, the lower 2-7 cm long, 4-16 mm wide, weakly bicolored, the basal and lowermost usually persistent, similarly

shaped cauline leaves continuing into at least the lower part of the capitulescence. Capitulescence continuous or usually strongly interrupted, with heads in short axillary to lateral glomerules; phyllaries often purple tinged, the outer basally woolly or partially buried in the wool of subtending bracts, ovate-triangular with attenuate-apiculate apices, $1/2-2/3$ as long as the inner, the inner 3.0-3.5 mm long, narrowly triangular to lanceolate with acute to obtuse, transparent or often with a golden sheen; receptacles deeply concave to crateriform, the centermost portion pronouncedly deep. Corollas usually with purple tips. Chromosome number, $n=14$ pairs.

South Texas to Florida and north, mostly along the Atlantic coast, the populations in northeastern México continuous with those of Texas, scattered in northern to central México, Nicaragua, widespread in South America, West Indies, Hawaii, Japan, Germany; commonly in disturbed habitats, often in areas of oak or pine woodlands; January-November or probably all year.

Recognized by its weakly bicolored, loosely woolly, obovate-spatulate leaves, similarly shaped ones continuing into at least the basal part of the capitulescence, which is usually strongly interrupted, its outer phyllaries basally woolly with very thin, acuminate-attenuate apices, and by its deeply crateriform receptacles.

4. *Gamochaeta purpurea* (L.) Cabrera, Bol. Soc. Argent. Bot. 9:377. 1961. BASIONYM: *Gnaphalium purpureum* L., Sp. Pl. 854. 1753. TYPE: UNITED STATES. "Carolina, Virginia, Pensylvania," *Kalm s.n.* (TYPE?: LINN fiche!).

Gnaphalium rosaceum I.M. Johnston, Contr. Gray Herb., ser. 2, 68:99. 1923. TYPE: MÉXICO. San Luis Potosí: Region of San Luis Potosí, 1878, Parry & Palmer 426 (HOLOTYPE: GH!).

Annuals or biennials. Stems erect to procumbent, 10-35 cm tall. Leaves oblanceolate, without a prominent petiolar region, often with closely sinuate margins, usually strongly bicolored, the lower 2-7 cm long, 7-16 mm wide, the basal and lowermost usually persistent, similarly shaped cauline leaves continuing into at least the lower part of the capitulescence. Heads usually in a continuous, or less commonly interrupted, capitulescence; phyllaries often purple tinged, the inner (3.5-)4.0-5.0 mm long, mostly lanceolate with acute to obtuse or rounded apices, the outer lightly woolly basally, ovate-triangular with acute apices, $1/2-2/3$ as long as the inner; receptacles concave but not deeply so. Corollas usually with purple tips. Chromosome number, $n=7$, 14 pairs.

Common and widespread in the eastern United States from eastern Texas to Florida, north to Kansas, Missouri, Michigan and New England, apparently disjunct to California and Oregon (see comments below), very scattered and apparently adventive elsewhere in the western United States, uncommon and

apparently adventive but scattered through México, Hawaii, New Zealand, South America (Brazil); weedy habitats; April-July(-August).

Gamochaeta purpurea is often confused with *G. pensylvanica* and *G. americana*, but it is probably most closely related to the latter, in its strongly bi-colored and thicker leaves, more condensed and typically uninterrupted spikes, and its relatively thick and shiny phyllaries. In the key above, however, it is contrasted with the former because of their similarity in the basally woolly, acute outer phyllaries and, in México, their tendency to produce purple pigments in the phyllaries and corolla tips. In the southeastern United States, plants of *G. americana* often have purplish phyllaries, though color is usually lacking in plants of México. Besides the differences noted in the couplet, the leaves and phyllaries of *G. pensylvanica* are much thinner textured than those of *G. purpurea*.

The plants of California and Oregon are essentially disjunct from those of the eastern United States and different in their slightly but distinctively narrower phyllaries with a thicker, more sharply differentiated stereome and longer, browner, hyaline apices. These ultimately may be found to have a different name or be undescribed, but their similarity to typical *Gamochaeta purpurea* is too great to add yet another new name without a more detailed study.

5. *Gamochaeta sphacilata* (Kunth) Cabrera, Bol. Soc. Argent. Bot. 9:380. 1961. BASIONYM: *Gnaphalium sphacilatum* Kunth, Nov. Gen. & Sp. 4[folio]:67. 1818; 4[quarto]:86. 1820. TYPE: MÉXICO. Edo. México: between México and Huehuetoca, *Humboldt & Bonpland s.n.* (HOLOTYPE: P fiche!). *Gnaphalium purpureum* L. var. *sphacilatum* (Kunth) Speg., Revist. Agron. La Plata 3:533. 1897. *Gnaphalium stachydifolium* Lam. var. *sphacilatum* (Kunth) Reiche, Anal. Univ. Chile 112:124. 1903.

Gnaphalium pedunculatum I.M. Johnston, Contr. Gray Herb., ser. 2, 68:99. 1923. TYPE: MÉXICO. Durango: Otinapa, 1906, *Palmer 411* (HOLOTYPE: GH!, photo! in *Rhodora* 37:449. 1935; Isotype: F!).

Annuals or biennials. Stems erect to ascending, 10-32 cm tall. Leaves linear to narrowly oblanceolate, 1-4 cm long, 1-3(-5) mm wide, the upper often folded, grayish to whitish green and evenly woolly above and beneath, the basal absent at flowering, the cauline continuing the whole length of the capitulescence, long, arcuate-spreading and standing nearly at right angles to the spike. Heads in a strongly interrupted spicate capitulescence of glomerules, axillary or on short, lateral branches, sometimes reduced to only a single, compact, terminal glomerule; outer phyllaries basally woolly or partly submerged in wool of subtending bracts, apically acuminate-attenuate, 1/2-2/3 as long

as the inner, the inner 4.0-5.0 mm long, brown tipped, the middle usually completely brownish.

In the United States known to me only by two collections from Jeff Davis county in the trans-Pecos area of Texas (*Turner 15546A* and *Worthington 14344*, both TEX), also western to south central México, similar plants seen from Colombia in northwest South America; often in area of pine-oak woods, openings or pastures; July-October. Cabrera (1978) included *Gamochaeta sphacilata* in the flora of Argentina.

Gamochaeta sphacilata is similar to *G. falcatum*, which also has narrow, gray-green leaves, equally pubescent above and beneath. As treated here, *G. sphacilatum* has whiter vestiture, a much more interrupted capitulescence with long, arcuate-spreading bracteal leaves, at least the phyllary apices dark brown, the middle phyllaries often completely brown, giving the whole capitulescence a dark color and the outer phyllaries with acuminate-attenuate apices. Further, *G. sphacilatum* apparently is less weedy than *G. falcatum* and occurs in rocky, rather than sandy habitats.

6. ***Gamochaeta ustulata*** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Gnaphalium ustulatum* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:404. 1841. LECTOTYPE (here designated): UNITED STATES. California: "Near St. Barbara in Upper California," *Nuttall s.n.* (BM-photo at GH!). *Gnaphalium purpureum* L. var. *ustulatum* (Nutt.) Boivin, Naturaliste Canad. 87:34. 1960. Nuttall also cited a specimen from "On the plains of the Platte, towards the rocky Mountains," but the California plant is the only one that could fit the description (see discussion below).

Gnaphalium pannosum Gandoger, Bull. Soc. Bot. France 65:42. 1918.

TYPE: UNITED STATES. Washington: not seen; not Schultz-Bip. 1845 or A. Gray 1883. As a synonym of *Gnaphalium ustulatum* fide Ferris (1959) and Drury (1971).

Perennial herbs from a relatively thick, horizontal, fibrous rooted rhizome. Stems 12-20 cm tall, densely white tomentose. Leaves obovate-spatulate, 2-5 cm long, 6-16 mm wide, densely and closely tomentose above and beneath but less so and darker colored above. the upper surface sometimes but not commonly glabrate, the basal persistent, cauline gradually reduced upward, continuing into only the basal part of the capitulescence. Heads in a dense, thick, uninterrupted, terminal spike or glomerule 1-6 cm long; phyllaries often all yellowish brown, darker at the apex, sometimes slightly purple tinged, the innermost 4-5 mm long, with apiculate apices, the outermost half as long, lightly woolly basally.

California in Santa Barbara and San Luis Obispo counties northward along the coast to Washington, Oregon and southwestern British Columbia, natural-

ized in New Zealand; various habitats very near the coast, dry hills, grasslands, sand hills, sandy ledges of cliffs in the spray zone; April-July.

As pointed out by Drury (1971), *Gamochaeta ustulata* has been overlooked by all recent Pacific coast floristicians, who have either completely deleted Nuttall's name or referred to it as a synonym of *G. purpurea*. Johnston (1924) argued that the species was separate from the latter on the basis of "gross habit and aspect," but his distinction apparently was not critical enough to be convincing. *Gamochaeta ustulata*, however, is an easy species to recognize, in that it is the only rhizomatous, truly perennial *Gamochaeta* in North America and has thicker leaves with a denser and more closely packed lower tomentum and browner, broader phyllaries than any other species with which it might be confused.

Nuttall's description of *Gnaphalium ustulatum* as perennial (" "), with leaves "whitely tomentose on both surfaces" leaves little doubt as to its true identity. Its closest relative may be *Gamochaeta stachydifolia* (Lam.) Cabrera, of Brazil, Uruguay and Argentina, which has a similar duration, habit and vestiture.

Drury (1971), whose illustration unequivocally shows the rhizomatous nature of the plants, saw specimens from California and British Columbia (Vancouver Island); there are specimens at LL-TEX from California, Oregon and Washington.

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**A NEW COMBINATION AND NEW SPECIES IN *GAMOCHAETA*
(ASTERACEAE: INULEAE) FROM CENTRAL AMERICA**

Guy L. Nesom

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

A new combination is proposed in the transfer of a Guatemalan endemic from *Gnaphalium* to *Gamochaeta*: ***Gamochaeta standleyi*** (Steerm.) Nesom. A new species, ***Gamochaeta irazuensis*** Nesom, is described from Costa Rica.

KEY WORDS: *Gamochaeta*, *Gnaphalium*, Asteraceae, Inuleae, Costa Rica, Guatemala.

In studies of *Gamochaeta* from North and Central America (Nesom 1990 and in prep.), one new combination among the Central American species is necessary. Additionally, a previously undescribed species from Costa Rica has come to light.

Gamochaeta standleyi (Steerm.) Nesom, *comb. nov.* **BASIONYM:** *Gnaphalium standleyi* Steerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:99. 1944. **TYPE:** GUATEMALA. Dept. Huehuetenango: Sierra de los Cuchumatanes, region of Chermal, alpine meadows, ca 3300 m, 28 Dec 1940, P.C. Standley 81097 (**HOLOTYPE:** F!).

Gamochaeta standleyi is a diminutive, subcaulescent, fibrous rooted annual, apparently endemic to the high mountains of northwest Guatemala. It is most similar in its phyllary morphology to *Gamochaeta purpurea* (L.) Cabrera but has much smaller leaves, that are densely and closely tomentose on both surfaces. *Gamochaeta purpurea* is an uncommon adventive in México and Central America.

Espinosa (1985) has identified plants from the high volcanic peaks immediately east of México City as *Gnaphalium standleyi*, but these belong to a different species (Nesom, in prep.) than the Guatemalan endemic here transferred to *Gamochaeta*.

Gamochaeta irazuensis Nesom, *sp. nov.* **TYPE:** COSTA RICA. Volcán Irazu, 10,000-11,330 ft (3030-3430 m), 1 Dec 1937-1 Jan 1938, P.H. Allen 702 (**HOLOTYPE:** F!).

Gamochaeta americanae (Mill.) Wedd. foliis bicoloribus et phyllariis aurei-fuscis glabris similis sed duratione perenni, habitu ascendenti vel decumbenti, absentia foliorum basaliū, et foliis minoribus amplitudis comparate aequatae differt.

Perennials from woody, fibrous rooted rhizomes. Stems densely matted white tomentose, ascending or decumbent-ascending, the lower producing numerous adventitious roots. Leaves narrowly elliptic-obovate, 7-22 mm long, 2-5 mm wide, clasping, strongly bicolored, densely matted white tomentose beneath, glabrescent above. Capitulescence of compact, uninterrupted, terminal, spiciform clusters 1-4 cm long. Heads campanulate-cylindric, 1.5-2.0 mm wide; phyllaries in 3-4 strongly graduated series, golden-brown, hyaline, the inner 3.5 mm long, narrowly oblong with an ovate-lanceolate, brown, terminal appendage, the outermost widely ovate, $1/3-1/4$ as long as the inner. Pistillate flowers 60-70. Hermaphroditic flowers 3-4, the corollas 2.2-2.4 mm long, glabrous; anthers tailed. Achenes 0.5-0.7 mm long, the surface densely invested with minute, rounded-conic, 2 celled, myxogenic trichomes; pappus bristles 17-21, basally united into a ring, easily caducous and released as a unit.

Known only from the type collection.

Gamochaeta irazuensis is similar to *G. americana* (Mill.) Wedd. in its bicolored leaves and completely glabrous, golden-brown phyllaries. The new species differs from the latter in its perennial duration, production of rhizomes, ascending-decumbent adventitious rooted stems, lack of persistent basal leaves, and smaller and relatively even sized cauline leaves. *Gamochaeta americana* is strictly annual, without rhizomes and produces a persistent rosette of basal leaves much larger than the cauline ones. Additionally, the pappus of *G. americana* can be seen under the compound scope to have a significantly more prolonged area of basal fusion than that of *G. irazuensis*.

Gamochaeta americana is widespread in México and Central America (Nesom 1990 and in prep.) and occurs at a wide range of elevations. Even at maximum elevations (up to 3200 m) for the species, however, it is always an annual. *Gamochaeta standleyi*, also, has either adopted or retained an annual duration in its adaptation to a high elevation habitat.

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A NEW SPECIES OF *LAENNECIA* (ASTERACEAE: ASTEREA) FROM
CHIHUAHUA, MÉXICO

Guy L. Nesom¹ & Joseph E. Laferrière²

¹Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.
and

²Department of Ecology and Evolutionary Biology, University of Arizona,
Tucson, Arizona 85721 U.S.A.

ABSTRACT

A new species, *Laennecia pimana* Nesom & Laferrière, is described. It apparently is narrowly endemic to the Sierra Madre Occidental of west central Chihuahua, México, and is most closely related to two other endemics of the same region, *Erigeron* (*Laennecia*) *eriophyllus* A. Gray and an as yet undescribed species of *Laennecia*. *Laennecia pimana* differs from these species by its eligulate pistillate corollas.

RESUMEN

Una nueva especie, *Laennecia pimana* Nesom & Laferrière, se describe. Posee un distribución muy restringida en la Sierra Madre Occidental del oeste de Chihuahua, México, y esta mas emparentada con otras especies endémicas de la misma región, *Erigeron* (*Laennecia*) *eriophyllus* A. Gray y una otra nueva especie de *Laennecia*. *Laennecia pimana* se diferencia de las anteriores por las corolas pistiladas eliguladas.

KEY WORDS: *Laennecia*, *Erigeron*, *Conyza*, Astereae, Asteraceae, México, Chihuahua.

Intensive collecting by the second author in west central Chihuahua has brought to light a previously undescribed species of *Laennecia*. The new species proposed here joins *Erigeron eriophyllus* A. Gray, which occurs from southern Arizona to eastern Chihuahua, and an undescribed species (a narrow endemic from west central Chihuahua), to form a trio of related species restricted in distribution primarily to northwestern México. Transfer of *E. eriophyllus* to *Laennecia*, description of the other new species, and the taxonomy of *Laennecia*, along with the rationale for considering it as a genus separate from *Conyza* are presented in a separate paper (Nesom 1990).

Laennecia pimana Nesom & Laferrière, *sp. nov.* TYPE: MÉXICO. Chihuahua: Mpio. Temosachic, 1 km E of Nabogame, 28° 30' N, 108° 30' W, pine-oak forest, 1800 m, 28 Oct 1988, J.E. Laferrière 2216 (HOLOTYPE: TEX; Isotype: MEXU)

Erigeron eriophyllus A. Gray similis vestimento lanato eglanduloso, foliis non-amplecticaulibus, et acheniis costis crassis; differt a *E. eriophyllus* foliis integris, acheniis glandulosis sed aliter glabris, pappo manifeste biserialis et corollis pistillatis sine ligulis.

Short lived perennials 45 cm tall, from a taproot. Stems, leaves and phyllaries gray lanose, eglandular, upper leaf surfaces equally as pubescent as the lower. Leaves narrowly oblong, sessile, entire, 15-25 mm long, 2.5-4.0 mm wide, barely if at all reduced in size upward. Heads 6-7 mm wide (pressed), in a few headed, spike like panicle, on peduncles 5-15 mm long; phyllaries purplish, narrowly triangular, in 3-4 slightly graduated series, the innermost 6-7 mm long, the inner with a herbaceous midregion extending to the base or nearly so, the margins indurated-hyaline. Pistillate corollas 2.5-3.0 mm long, tubular-filiform, eligulate, apically fimbriate, much shorter than the style and style branches. Disc corollas slightly pubescent on the throat, eglandular, 4.3-5.0 mm long, the tube 3.0-3.5 mm long, ampliate immediately below the insertion of the lobes, the lobes 0.8-1.0 mm long, narrowly triangular-lanceolate, spreading-recurved. Achenes obovate, 1.9-2.2 mm long, 0.8-1.0 mm wide, strongly flattened, the faces tan, glabrous except for a few, but prominent, sessile, resin glands near the apex, completely ringed by a thick, white rib; pappus of 33-39 slender, barbellate bristles 3.8-4.5 mm long, with an outer series of setae or bristles 0.3-0.5 mm long. Chromosome number unknown.

Known only from the type collection.

Laennecia pimana is named for the Mountain Pima inhabitants of the Sierra Madre. It is similar to *Erigeron eriophyllus* and the undescribed species in its lanose, eglandular vestiture, nonclasping leaves and thick ribbed achenes, but it is different from both in its eligulate pistillate corollas. It differs from *E. eriophyllus* in its entire leaves, apically glandular but otherwise glabrous achenes and prominently biseriate pappus. It differs from the undescribed species in its smaller achenes and pappus of fewer bristles.

The type locality is a mixed pine-oak forest dominated by *Pinus engelmannii* Carr., *Quercus chihuahuensis* Trel. and *Q. viminea* Trel. Typical plants of *Erigeron eriophyllus* (A. Gray) Nesom (Laferrière 1570, ARIZ) have been collected in the immediate vicinity.

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TAXONOMY OF THE GENUS *LAENNECIA* (ASTERACEAE: ASTEREAE)

Guy L. Nesom

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

A group of 15 Mexican and South American species that have been regarded as *Conyza* are transferred to the genus *Laennecia*, which is divided into two sections, sect. *Laennecia* and sect. *Sophiifolium* Nesom. The species of *Laennecia* are generally characterized by phyllaries with a single midvein that is greenish rather than orange resinous, deeply lobed disc corollas and the presence of achenial glands. Most of the species also have herbage with a resinous glandular, woolly vestiture. Three species are already identified as *Laennecia*: *L. filaginoides* DC, *L. gnaphalioides* (Kunth) Cass. (the generitype) and *L. pimana* Nesom & Laferrière. Nomenclatural transfers for the remainder are proposed here: *L. altoandina* (Cabrera) Nesom, *L. artemisiifolia* (Meyen & Walp.) Nesom, *L. confusa* (Cronq.) Nesom, *L. coulteri* (A. Gray) Nesom, *L. eriophylla* (A. Gray) Nesom, *L. lasseriana* (Aristeg.) Nesom, *L. microglossa* (S.F Blake) Nesom, *L. mima* (S.F. Blake) Nesom, *L. prolialba* (Cuatr.) Nesom, *L. schiedeana* (Less.) Nesom and *L. sophiifolia* (Kunth) Nesom. In addition, a new species from Chihuahua, México, is described as *L. chihuahuana* Nesom. An hypothesis of infrageneric phylogeny is presented, based on a cladistic analysis. The generic relationships of *Laennecia* are not clear, but it may be more closely related to the Old World genus *Nidorella* or even members of the subtribe Grangeinae than to true *Conyza* and *Erigeron*.

KEY WORDS: *Conyza*, *Laennecia*, Astereae, Asteraceae, México.

Zardini (1981) proposed that Cassini's genus *Laennecia* be reseedgregated from *Conyza* with two species, *L. filaginoides* DC. and *L. gnaphalioides* (Kunth) Cass (the generitype). She separated *Laennecia* and *Conyza* by the following key (translated).

- 1. Plants generally not woolly; achenes with duplex trichomes very sparse; pappus uniseriate *Conyza*
- 1' Plants woolly; achenes with duplex trichomes dense or covering only the central part and margins; pappus biseriate *Laennecia*

Using the same criteria, Cuatrecasas (1969) previously recognized the two species as *Conyza* sect. *Laennecia* (Cass.) Cuatr. I agree that two groups exist within American *Conyza* as that genus is now generally perceived and that these criteria point in the right direction for their recognition. Most of the species that correctly belong in *Laennecia*, however, are eliminated by adherence to Cuatrecasas' and Zardini's strict concept of the group. Instead, there appears to be a monophyletic group of not two, but 15 species centered around *L. filaginoides*. The number of pappus series (1 or 2) in these species is variable, as is the arrangement of achenial pubescence (dense to completely lacking) and even the woolly vestiture. These species are interrelated in discernible patterns among themselves, however, and distinguished as a group from true *Conyza* by a combination of characters as presented in the following couplet.

1. Plants variously pubescent but not woolly; glands, if present, stipitate and not resin tipped; phyllaries 3 veined except in smallest heads, at least the midvein strongly orange resinous; disc corollas strongly orange veined, with shallow, deltate lobes cut 1/5-1/8 to the base of the limb; achenes eglandular, sparsely strigose to glabrate; pappus uniseriate *Conyza*
- 1' Plants woolly, less commonly hirsute-pilose; short stipitate glands at least on the leaves of most species, these developing prominent, orange resinous heads; phyllaries with a green midregion, the single, thin midvein sometimes yellowish but not orange resinous; disc corollas light veined, not orange, with lanceolate lobes cut 1/2-3/4 to the base of the limb; achenes usually glandular, sometimes eglandular, densely sericeous to strigose or glabrous; pappus uniseriate or strongly biseriate *Laennecia*

Laennecia and *Conyza* have been regarded as congeneric on the basis of their joint possession of eligulate or short ligulate pistillate flowers in numerous series and their achenes with pappus bristles that elongate at fruit maturity. Based on the evidence presented here, however, these similarities probably should be interpreted as the results of parallel or convergent evolution, because *Laennecia* can be recognized as a clearly delimited lineage separate from *Conyza* and perhaps not particularly closely related to it.

The orange resinous midveins of the phyllaries, which are invariably present in *Conyza* and *Erigeron* (Nesom 1990), are absent in *Laennecia*. This difference is so strong that an individual of the latter can be separated from *Conyza* on the basis of no more than a single phyllary. The same is true for the striking difference in the morphology of the disc corollas. The deeply lobed, often goblet shaped corollas of *Laennecia* are more similar to those of *Baccharis* and other South American genera of Astereae in this respect than they are to those of *Conyza* and most North American genera.

Among the distinctive features of *Laennecia*, the glandularity does not occur in any species of *Conyza*, at least as the genus is understood in the New World. Stipitate glandular hairs occur commonly on the vegetative parts of *Erigeron* (e.g., *E. oreophilus* Greenm. and many other species) and rarely on *Conyza* (e.g., *C. coronopifolia* Kunth) but the glands of *Laennecia* with a head of yellowish orange, transparent resin is different from anything seen in either of those genera. All of the glands are "Type C" trichomes (Nesom 1976), which apparently are common throughout the tribe, but in *Laennecia* they produce the extra "head" of translucent resin. The same is true of the achenes, where late in their ontogeny, the glands of the more advanced species of *Laennecia* develop particularly large, resinous heads.

To my knowledge, glandular achenes occur in only a few species of other North American genera of Astereae. None are found in *Conyza* or in the large genus *Erigeron*, which is considered to be closely related to *Conyza*. They do occur in a few species of *Aster* and *Chrysothamnus* and in at least one species of *Haplopappus* sect. *Macronema*.

Glandular achenes are characteristic of genera of the subtribe Grangeinae, and it is possible that the recent evolutionary ancestry of *Laennecia* is more closely linked to that group than with *Conyza*. As pointed out by De Jong (1965), plants of the Grangeinae also tend to produce tubular, often eligulate pistillate flowers in several series. *Laennecia* is excluded from the strictly defined Grangeinae of Fayed (1979), however, as well as a more broadly defined subtribe, because of its pappus of barbellate bristles. Almost all of the American genera of Grangeinae centered around *Lagenophora* (Cabrera 1966) have epappose or bristleless achenes. On the other hand, significant variation in the nature of the pappus is known to occur even within many genera of Astereae and the lack of bristles probably should not be disproportionately weighted in the definition of the Grangeinae. In fact, the monotypic *Floscaldasias* of South America, accepted by Grau (1977) in the Grangeinae, has 1-2 series of numerous pappus setae that are as long as the disc corollas.

Alternatively, a possible relationship between *Laennecia* and the Old World genus *Nidorella* should be investigated in more detail. *Conyza* in the Old World appears to be polyphyletic and includes species that probably are most closely related to species of *Nidorella* (Nesom 1990). Achenes of *Nidorella* are glandular, but on the other hand, the disc corollas of those species are also glandular and are deltate, features not characteristic of *Laennecia*.

Laennecia Cass., Dict. Sci. Nat. 25:91. 1822. Type species: *Conyza gnaphaloides* Kunth. *Conyza* sect. *Laennecia* (Cass.) Cuatr., Webbia 24:206 1969. Not *Conyza* sect. *Laennecia* (Cass.) Cuatr., Phytologia 9:1. 1963 (comb. illeg.).

Taprooted annuals, biennials, or short lived perennials (fibrous rooted in *L. confusa* [Cronq.] Nesom). Leaves, stems and phyllaries white tomentose

or cottony, coarsely hairy in 2 species, glandular with sessile, translucent, orange-yellow, resin glands, eglandular in 4 species. Leaves alternate, toothed to pinnately lobed, rarely entire, sessile, clasping or nonclasping. Heads in spicate or racemose to loosely panicate or corymbose capitulescences; buds erect. Pistillate flowers numerous in several series, fertile, white, filiform-tubular, eligulate and apically fimbriate, much shorter than the style, or some species with a ligule 0.2-2.5 mm long. Hermaphroditic (disc) flowers fertile, cream to yellowish, narrowly tubular-funnelform, amplate near the origin of the lobes, the lobes triangular-lanceolate, 1/2-3/4 the total length of the limb (longer than the throat), eglandular but usually with a few, viscid, clavate hairs on the limb; style branch appendages deltate to narrowly triangular. Achenes compressed, narrowly oblanceolate-elliptic to obovate in outline, with sessile resin glands on the faces, rarely eglandular, minutely and sparsely short stipitate glandular in sect. *Sophiifolium* Nesom; pappus uniseriate or biseriate, a series of slender barbellate, often easily caducous bristles, usually elongating at maturity past the disc corollas and involucre, with or without an outer series of much shorter setae, bristles, or scales. Base chromosome number, $x=9$.

Laennecia is restricted to the New World, where its species occur primarily in montane habitats or at least in temperate highlands rather than tropical habitats. Population systems within several of the species are widely disjunct: *L. gnaphalioides*, *L. filaginoides* and *L. sophiifolia* (Kunth) Nesom between North/Central America and South America; *L. schiedeana* (Less.) Nesom and *L. confusa* between west to northwest México, and south central México/Central America.

The genus is formally divided into two sections. The rationale for this partition is presented below in connection with the phylogenetic analysis.

Laennecia sect. *Laennecia*.

Leaves mostly oblong-lanceolate, toothed, glandular or eglandular, herbage glandular or eglandular, with densely white tomentose vestiture. Achenes with large, sessile, persistent resin glands, eglandular in one species.

Species included: *Laennecia chihuahuana* Nesom, *L. confusa*, *L. eriophylla* (A. Gray) Nesom, *L. filaginoides*, *L. gnaphalioides*, *L. lasseriana* (Aristeg.) Nesom, *L. microglossa* (S.F. Blake) Nesom, *L. mima* (S.F. Blake) Nesom, *L. pimana* Nesom & Laferrière, *L. prohalba* (Cuatr.) Nesom and *L. schiedeana*.

***Laennecia* sect. *Sophiifolium* Nesom, sect. nov.** Type species: *Conyza sophiifolia* Kunth, *Nov. Gen. & Sp.* 4[folio]:56. 1818; 4[quarto]:72, pl. 326. 1820.

Folia pinnatifida vel bipinnatifida (in *Laennecia coulteri* plerumque dentata), glandulosa, vestimento hirsuti-piloso. Achenia glandibus parvis parum elevatis deciduis.

Leaves mostly pinnatifid to bipinnatifid (toothed in *Laennecia coulteri*), glandular, with hirsute-pilose vestiture. Achenes with small, sometimes slightly raised, apparently deciduous glands.

Species included: *Laennecia altoandina* (Cabrera) Nesom, *L. artemisiifolia* (Meyen & Walp.) Nesom, *L. sophiifolia* and provisionally, *L. coulteri* (A. Gray) Nesom (see comments below).

SPECIES RELATIONSHIPS

The genus was analyzed cladistically (Wagner parsimony of PAUP: Swoford 1985) using 14 characters that could be unequivocally scored for the 15 species. The single tree obtained is 18 steps long, but on the cladogram (Figure 1) I have added a 19th, homoplasious, step by keeping the "*mima/lasseriana*" branch separate from the "*sophiifolia*" lineage. The change involved (apparent loss of ligule) apparently is an easily modifiable genetic feature under simple control, since it has occurred in parallel on three additional branches. The tree was rooted at a position to emphasize the difference between the taxa with a woolly-tomentose vestiture and toothed leaves (sect. *Laennecia*, see below) and those with a more hirsute vestiture and mostly pinnatifid leaves (sect. *Sophiifolium*). The polarity of all except one of the character states in Table 1 has been inferred from the position of the root. I have regarded woolly vestiture as apomorphic, primarily because it appears developmentally more complex than nonwoolly. If, in reality, the reverse were true, it would slightly shift the root position to the base of the four species of the *Laennecia schiedeana* group and strengthen the otherwise weak link between *L. coulteri* and the species with pinnatifid leaves.

In this view of the phylogeny (Figure 1), the woolly taxa from high elevation habitats in northern South America, *Laennecia mima*, *L. lasseriana*, *L. prolialba* and including the more widespread *L. schiedeana*, form a primitive subgroup of sect. *Laennecia*. The latter species is variably hirsute-pilose to densely woolly, somewhat intermediate in this respect between the two sections.

The remainder of sect. *Laennecia* is restricted to North America, except for *L. filaginoides* and *L. gnaphalioides*, which also occur in South America, probably secondarily. Three endemics, primarily of northwestern México, *L. eriophylla*, *L. chihuahuana* and *L. pimana*, are the most advanced in this lineage. They are similar among themselves in their large achenes with thick, white ribs and their nonclasping, eglandular leaves. *Laennecia confusa* is similar to these in its nonclasping, eglandular leaves, but it has smaller, thin nerved achenes with relatively few pappus bristles and, alone in the genus, it produces fibrous roots. *Laennecia gnaphalioides* also forms large, distinctively thick ribbed achenes and is closely related to these species. *Laennecia filaginoides*, with its large number of pappus bristles and strongly developed outer

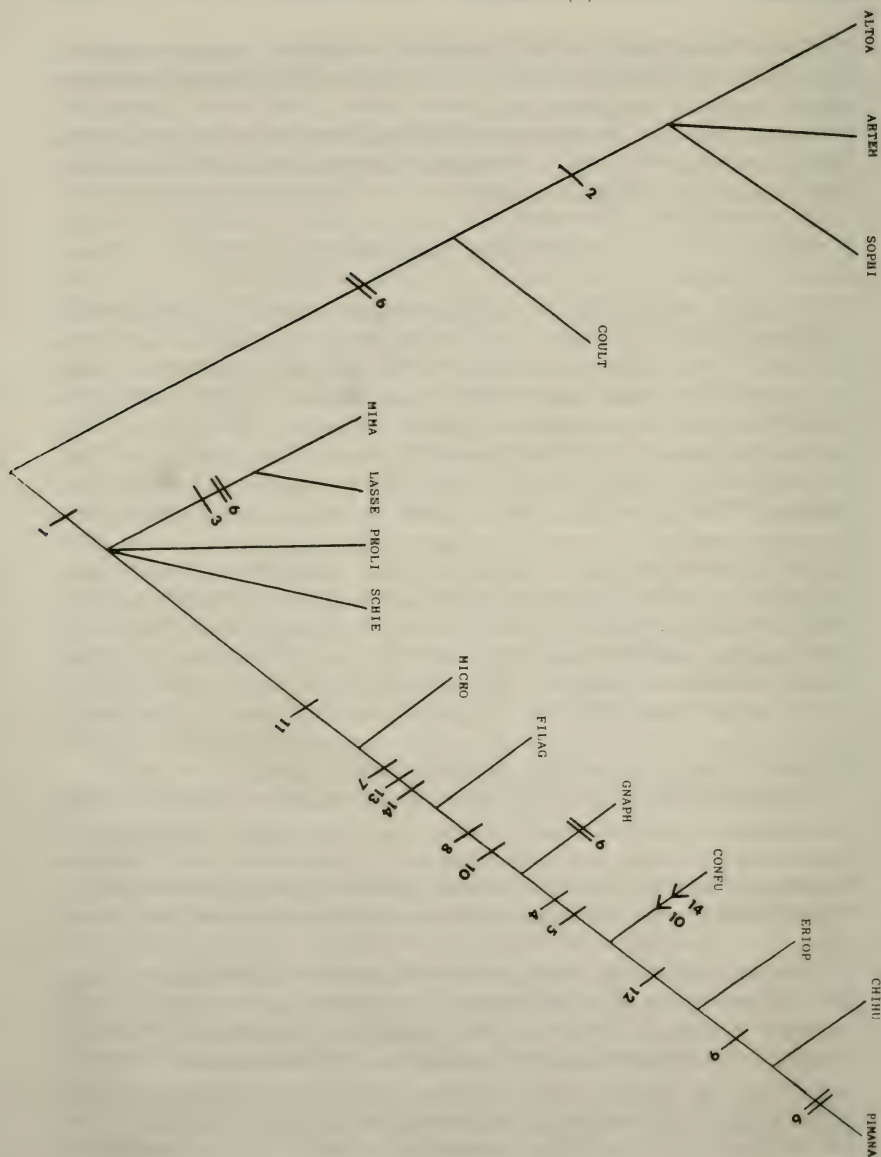


Figure 1. Cladistic relationships of the species of *Laennecia*. Numbers represent characters as listed in Table 1. Slash = synapomorphy; double slash = parallel synapomorphy; down arrow = reversal.

Table 1. Characters and character states of *Laennecia* used in the cladistic analysis (see discussion). Data matrix is shown in Table 2.

1. Vestiture (0) woolly (1) strigose-hirsute
2. Leaf margins (0) toothed (1) deeply pinnatifid
3. Leaf margins (0) flat, toothed to pinnatifid (1) revolute, nearly entire
4. Leaf bases (0) clasping (1) non-clasping
5. Leaves (0) glandular (1) eglandular
6. Ligules (0) present (1) absent
7. Style branch appendages (0) deltate (1) triangular-lanceolate
8. Achenial glands (0) non-resinous (1) with an expanded, apical, resin drop
9. Achenial hairs [Zwillingshaare] (0) present (1) completely absent
10. Achene ribs (0) thin (1) prominently thickened
11. Achene size (0) 0.8-1.5 mm long (1) at least some longer than 1.5 mm
12. Achene size (0) 0.8-1.9 mm long (1) 2.1-2.5 mm long
13. Number of pappus series (0) 1 (1) 2
14. Number of pappus bristles (0) 9-20 (1) [20-] 33-75

pappus, also is closely related to this group. The pappus of *L. microglossa* sometimes can be observed to have an "outer" series of a few, thin setae, but it is not nearly so prominent as in the other primarily Mexican taxa of sect. *Laennecia*. Among the species restricted to México, *L. microglossa* and *L. coulteri* appear to be the most primitive.

In sect. *Sophiifolium*, *Laennecia artemisiifolia* and *L. altoandina*, are endemic to southern South America. *Laennecia sophiifolia* is widespread in México and in Andean South America but apparently absent from most of Central America. Its deeply pinnatifid leaves suggest that its geographical origin was similar to the two South American endemics. *Laennecia coulteri* is provisionally included in sect. *Sophiifolium* on the basis of its essentially nonwoolly vestiture, eligulate ray flowers and the observation that its leaves sometimes, though uncommonly, are deeply toothed. It occurs only in North America and at relatively low elevations, and is morphologically similar to sect. *Laennecia* in its toothed leaves and tendency to produce a subwoolly (but mostly pilose-hirsute) vestiture. McVaugh (1984) also noted that a close similarity exists between *L. coulteri* and *L. sophiifolia*.

Table 2. Taxa of *Laennecia* with character states used in cladistic analysis.

TAXON	CHARACTER
	12345678901234
schie	00000000000000
proli	00000000000000
mima	00100100000000
lasse	00100100000000
eriop	00011011011111
chihu	00011011111111
piman	00011111111111
confu	00011011001010
gnaph	00000111011011
flag	00000010001011
micro	00000000001000
coul	10000100000000
sophi	11000100000000
artem	11000100000000
altoa	11000?00000000

Critical observations on types and typification of *Laennecia flaginoides* and *L. gnaphalioides* are found in Cuatrecasas (1969) and Zardini (1981). Taxonomic notes on *L. schiedcana* and other species are found in Blake (1917), Cuatrecasas (1970) and McVaugh (1984).

ARTIFICIAL KEY TO THE SPECIES OF *LAENNECIA*

1. Pistillate flowers ligulate(2)
- 1' Pistillate flowers eligulate(7)
 2. Leaves and phyllaries with sessile, resin glands; leaves clasping .(3)
 - 2' Leaves and phyllaries eglandular; leaves not clasping(5)
3. Plants perennial, from South America *L. prolialba*
- 3' Plants annual, from North and Central America(4)

4. Stems basally branched and decumbent; herbage densely white woolly, completely obscuring the stems immediately below the heads; disc corollas 2.4-2.5 mm long *L. microglossa*
- 4' Stems unbranched and strictly erect at the base; herbage variably woolly but never so densely so as to obscure any part; disc corollas 2.8-3.2 mm long *L. schiedeana*
5. Plants fibrous rooted; achenes 1.4-1.8 mm long; pappus bristles 14-22; Sinaloa and Chihuahua south through Guerrero and San Luis Potosí to Chiapas and Guatemala *L. confusa*
- 5' Plants taprooted; achenes 2.5-3.0 mm long; pappus bristles 35-75 (6)
 6. Ligules 0.5-0.8 mm long, purple; achenes eglandular, strigose on the faces and thick, white margins; pappus of 35-45 bristles, essentially uniseriate or with a few, outer setae 0.3 mm long; southern Arizona to west central Chihuahua *L. eriophylla*
 - 6' Ligules 1.0-2.0 mm long, white; achenes with glands scattered over both faces or concentrated near the apex, without other vestiture; pappus of 60-75 bristles, with an outer series of linear scales 0.5-0.8 mm long; west central Chihuahua *L. chihuahuana*
7. Stems and leaves densely and prominently woolly-tomentose (8)
- 7' Stems and leaves coarsely hairy but not at all woolly-tomentose (13)
 8. Plants of South America (9)
 - 8' Plants of North and Central America (11)
9. Achenes densely silky-strigose, the surface completely obscured *L. filaginoides*
- 9' Achenes sparsely strigose, the surface not obscured (10)
 10. Annuals, densely tomentose but the stem and leaf surfaces not completely obscured; phyllaries glandular and sparsely villous, the inner 4-5 mm long, with broad, hyaline margins *L. mimia*
 - 10' Perennials, with a dense, white tomentum completely obscuring the stem and leaf surfaces; phyllaries glandular but otherwise glabrous, the inner 3.5 mm long, with the margins little differentiated from the middle portions *L. lasseriana*
11. Achenes usually purplish, completely covered with a silky strigose pubescence, without thick, marginal ribs *L. filaginoides*

- 11' Achenes tan, glabrous or silky strigose only on the margins and in a central patch on each face, with thick, white, marginal ribs (12)
12. Leaves eglandular, not clasping; heads 6-7 mm wide; achenes glandular but otherwise glabrous; pappus bristles 33-39 *L. pimana*
- 12' Leaves glandular, clasping; heads 8-12 mm wide; achenes glandular, silky strigose on the margins and with a central patch of hairs on each face; pappus bristles 20-24 *L. gnaphalioides*
13. Plants of North and Central America (14)
- 13' Plants of South America (15)
14. Leaves not clasping, often narrowed to a petiolar base, usually bipinnatifid, sometimes merely pinnatifid *L. sophiifolia*
- 14' Leaves distinctly clasping, barely if at all reduced in width proximally, toothed, never bipinnatifid *L. coulteri*
15. Leaves pinnately shallowly lobed; phyllaries broadly elliptic, apically obtuse; disc corollas 1.5 mm long *L. altoandina*
- 15' Leaves pinnatifid to bipinnatifid; phyllaries linear-lanceolate, apically acute; disc corollas 2.2-3.4 mm long (16)
16. Stems erect; heads 1.5-2.5(-4.0) mm wide, the inner phyllaries 2.5-3.0 mm long; disc corollas 2.2-2.6 mm long; pistillate corollas 0.8-1.2 mm long *L. sophiifolia*
- 16' Stems decumbent; heads 4-5 mm wide, the inner phyllaries 3.0-3.5 mm long; disc corollas 2.5-3.4 mm long; pistillate corollas 1.5-1.8 mm long *L. artemisiifolia*

TAXONOMIC SUMMARY

1. ***Laennecia altoandina*** (Cabrera) Nesom, *comb. nov.* BASIONYM: *Conyza altoandina* Cabrera, Bol. Soc. Argent. Bot. 14:347. 1972. TYPE: ARGENTINA. Prov. Jujuy: Dep. Capital, entre León y Nevado de Chani, Esquina, *Fabris, et al. 4132* (HOLOTYPE: LP).

Short lived perennials with decumbent-ascending branches, sessile glandular and moderately villous-hirsute. Leaves subclasping, shallowly pinnatifid with a broad midregion or deeply 2-4 toothed, 1-2 cm long, 5-8 mm wide. Heads 4-5 mm wide, sessile or subsessile in a leafy, spicate, few headed panicle; phyllaries in 2-3 subequal series, with the inner 2.5-3.0 mm long, the outer broadly ovate, with broad hyaline margins and obtuse apices. Disc corollas

1.5 mm long. Achenes oblong-obovate, 1.2 mm long, glabrous to very sparsely strigose.

Argentina, in mountains of the Provincia de Jujuy; ca 4000 m.

I have not seen specimens of *Laennecia altoandina*, but judging from the description, illustration and contrasts in the key provided by Cabrera (1978), it is a member of *Laennecia* and distinct from the other species. In the Jujuy Province, where *L. altoandina* apparently is endemic, the closely related *L. artemisiifolia* and *L. sophiifolia* also occur.

2. *Laennecia artemisiifolia* (Meyen & Walp.) Nesom, *comb. nov.* BASIONYM: *Conyza artemisiifolia* Meyen & Walp., Nov. Act. Acad. Caes. Leop. 19(Suppl. 1):262. 1843. TYPE: ARGENTINA, not seen. *Erigeron artemisiifolia* (Meyen & Walp.) Schultz-Bip., Bull. Soc. Bot. France 12:81. 1865.

Conyza andicola Philippi, Anal. Mus. Nac. Chile, Bot. 8:38. 1891. TYPE: CHILE, not seen. Not *Erigeron andicola* DC. As synonym *fide* Cabrera (1978).

Erigeron senecioides Wedd., *Chloris Andina* 1:198. 1856. TYPE: PERÚ, not seen. *Conyza senecioides* (Wedd.) Cabrera, Revista Invest. Agric. Bs. Aires 11:403. 1957. As synonym *fide* Cabrera (1978).

Taprooted annuals or short lived perennials, usually with several, prostrate to decumbent-ascending stems from the base. Stems, leaves and phyllaries with minute, sessile or short stipitate resin glands, also sparsely to moderately pubescent with thick based, multicellular, long attenuate, eglandular hairs, these sometimes becoming somewhat villous, also with much smaller, viscid-glandular but not stipitate hairs. Leaves pinnatifid to bipinnatifid, sessile to subclasping, sometimes slightly auriculate at the base, 1-2(-3) cm long. Heads 3-5 mm wide, on pedicels 0.5-2.0 mm long, in compact, spicate panicles; phyllaries narrowly triangular-lanceolate, in 2-4 equal to subequal series, the inner 3.0-3.5 mm long, the outer strigose with thick, multicellular, eglandular hairs, sessile glandular at least proximally, the margins broad and hyaline, with hyaline, long attenuate, and often purple apices. Pistillate corollas 1.5-1.8 mm long, eligulate, the stigma and style extending 0.8-1.0 mm above the corolla. Disc corollas 2.5-3.4 mm long, the tube 1.6-2.0 mm long, Achenes oblong-obovate, 0.8-1.2 mm long, thin nerved, sparsely strigose, with at least a few sessile, resin glands, these often clustered at the apex; pappus a single series of 11-15 fragile bristles 3.0-3.8 mm long at maturity.

Perú, Bolivia, Chile, Argentina; open rocky, sandy, or grassy sites, often in fallow fields or other disturbed sites; 3200-4200 m; flowering (January-) February-May.

Laennecia artemisiifolia is closely similar to *L. sophiifolia* but distinguished by its high elevation habitats, decumbent stems, and larger heads and corollas.

3. *Laennecia chihuahuana* Nesom. *sp. nov.* TYPE: MÉXICO. Chihuahua: Mpio. Ocampo, Parque Nacional de Cascada Basaseachic, [ca 4.5 km S of village of Basaseachic], on nearly barren rock at overlook ca 1 km airline S of Cascada, with *Arctostaphylos pungens*, *Quercus* cf. *crassifolia*, *Q. coccolobifolia*, sparse grasses; ca 2100 m, 3 Oct 1986, R. Spellenberg, *et al.* 8695 (HOLOTYPE: NMC!; Isotypes: ESAH, MEXU, TEX!, UC).

Erigeron eriophyllus A. Gray similis sed ligulis albis longioribus, acheniis glandulosis sed aliter glabris, et setis pappo numerosioribus differt.

Short lived perennials, 25-40 cm tall, from a slender, woody taproot. Stems, leaves and phyllaries closely gray woolly, eglandular, the phyllaries and upper leaf surfaces glabrescent to glabrate. Leaves narrowly oblong to linear-ob lanceolate, sessile, entire or with a few, shallow teeth, 10-30 mm long, 1-3 mm wide, slightly reduced in size upward. Heads 8-10 mm wide (pressed), in panicles or loose corymbs, on peduncles mostly 1-3 cm long; phyllaries in 3-4 graduated series, the innermost 7.0-7.5 mm long, the inner with a narrow, green midregion extending to the base or nearly so, the margins indurated-scarious, often purplish. Pistillate corollas 6.0-6.5 mm long, the ligules prominent, 1.0-2.0 mm long, 0.3-0.5 mm wide, white. Disc corollas glabrous with a few hairs, white to cream, 5.0-5.5 mm long, the tube 3.0-3.5 mm long, throat gradually ampliate, the lobes 0.5-0.7 mm long. Achenes obovate to widely obovate, 2.5-3.0 mm long, 1.3-1.5 mm wide, strongly flattened, the faces tan, with thick, white margins, the whole surface sparsely glandular with sessile resin glands, or the glands sometimes concentrated near the neck, without other vestiture; pappus of 60-75 thickened, minutely barbellate bristles 5.0-5.5 mm long, with a prominent outer series of linear to narrowly triangular scales 0.5-0.8 mm long. Chromosome number unknown.

Known only from the vicinity of Basaseachic in west central Chihuahua, México; oak or oak-pine woods; 2000-2100 m; September-November.

Additional collections examined: MÉXICO. Chihuahua: Mpio. Creel, Cusare, S of Creel, open, grazed slope, top of gully eroded area, 14 Sep 1973, *Bye 5038* (TEX); Mpio. Ocampo, Parque Nacional de Cascada Basaseachic, headwaters of Río Mayo: pine-oak forest above waterfall, 2000 m, 2 Oct 1983, *Martin & O'Rourke s.n.* (ARIZ); above falls near parking lot, 2000 m, 14 Oct 1985, *Martin s.n.* (ARIZ); ca 3 km S of village of Basaseachic, steep, E facing slope with large boulders and rock faces, above river and trail to falls, grassy area among *Pinus*, *Cupressus*, shrubby oaks and dominant *Garrya*, ca 2050 m, 19 Oct 1986, *Nesom & Vorobik 5690* (MEXU, TEX).

Laennecia chihuahuana is characterized by a taproot, woolly but eglandular stems, leaves and phyllaries, ligulate pistillate corollas, large, thick ribbed and glandular but otherwise glabrous achenes, and a biseriate pappus of 60-75

bristles with a prominent outer series of scales. It is most closely related to *L. criophylla*, *L. pimana* and *L. confusa*, which are united as a group by their woolly but nonglandular herbage and their sessile but nonclasping leaves.

4. ***Laennecia confusa*** (Cronq.) Nesom, *comb. nov.* BASIONYM: *Conyza confusa* Cronq., Bull. Torrey Bot. Club 70:632. 1943. Based on: *Erigeron gnaphalioides* Kunth, *Nov. Gen. Sp.* 4[quarto]:88. 1820; 4[folio]:69. 1818. *Stenactis gnaphalioides* (Kunth) Cass., *Dict. Sci. Nat.* 1:484. 1827. *Heterochaeta gnaphalioides* (Kunth) DC., *Prodr.* 5:282. 1836. Non *Conyza gnaphalioides* Kunth (\equiv *Laennecia gnaphalioides* [Kunth] Cass.). TYPE: MEXICO. Guanajuato: *Humboldt & Bonpland s.n.* (HOLOTYPE: P, fiche!).

Perennials, fibrous rooted, the whole plant woolly. Leaves densely white beneath, green glabrate to much less hairy above, eglandular, the basal usually persistent, the cauline narrowly oblong-elliptic, not clasping, entire to few toothed. Capitulescence a narrow, spike like panicle or sometimes the heads few and on long, divergent-ascending peduncles; pistillate corollas with a white ligule 0.5-2.5 mm long. Achenes 1.0-1.8 mm long, with thick margins, sparsely pilose or strigose, rarely glabrous, usually prominently papillate glandular on the faces, at least near the apex; pappus of 14-22 bristles, with an outer series of bristle like setae 0.1-0.3 mm long. Chromosome number, $n=9$ pairs.

Sinaloa, Chihuahua, Durango, Nayarit, Zacatecas, Jalisco, Michoacán, Guanajuato, Guerrero, México, San Luis Potosí. apparently disjunct to Chiapas and Guatemala; clearings or meadows among pines or pine-oak; 1500-2750 m; August-November.

Within *Laennecia confusa*, there appear to be two elements that may ultimately be recognized as separate species. From Guatemala north to southern Durango, the achenes are narrowly elliptic, sparsely but evenly strigose and evenly glandular. In northern Durango and southern Chihuahua, the achenes are obovate, strigose only on the margins and the glands are clustered near the apex. In both forms, however, there are never more than 22 pappus bristles and the achenes are less than 2.0 mm long.

5. ***Laennecia coulteri*** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Conyza coulteri* A. Gray, Proc. Amer. Acad. Arts 7:355. 1868. Syntypes (as cited by Gray): UNITED STATES. [Arizona or California]: *Coulter 285 & 286* (GH, not seen). *Conyzella coulteri* (A. Gray) E. Greene, *Fl. Francisc.* 386. 1897. *Eschenbachia coulteri* (A. Gray) Rydb., Bull. Torrey Bot. Club 33:154. 1906.

Erigeron discoideus Kellogg, Proc. Calif. Acad. Sci. 5:55. 1873. TYPE: UNITED STATES. California: Island of the San Juan River, Webb's Landing, late autumn 1872, *Kellogg s.n.* (Not seen). As synonym *fide* Ferris (1960).

Taprooted annuals, moderately to densely pubescent with jointed hairs of varying lengths. Leaves 2-15 mm wide, regularly toothed or shallowly lobed, clasping to subclasping, with papillate sessile resin glands. Capitulescence a spike like panicle to broader, more elliptic or nearly corymbose in shape. Phyllary apices long acuminate and membranous. Pistillate corollas eligulate. Achenes light tan, sparsely strigose, 0.8-1.2 mm long, 0.3 mm wide, usually with minute, short stipitate to sessile glands; pappus uniseriate, of 9-16 bristles. Chromosome number, $n=9$ pairs.

Baja California Norte, Sonora, Chihuahua, Durango, Zacatecas, Jalisco, Coahuila, Nuevo León, San Luis Potosí, Tamaulipas and the adjacent United States (Texas, Colorado, New Mexico, Arizona, Nevada, California); roadsides, fields, grasslands, moist meadows, brushy plains and rocky deserts, often associated with *Larrea*, *Agave*, *Prosopis* and *Acacia*; (5-)1250-2350(-2700) m; (February-)May-November.

Laennecia schiedeana is superficially similar to *L. coulteri* and might be confused in identification with it. *Laennecia coulteri* is distinguished from the former by the lack of well developed arachnoid pubescence, larger, more toothed vs pinnatifid leaves, broader capitulescences, distinctive phyllary apices, eligulate pistillate corollas and slightly smaller achenes. In addition, it is a species of much lower elevations and more arid habitats.

6. *Laennecia eriophylla* (A. Gray) Nesom, *comb. nov.* BASIONYM: *Erigeron eriophyllus* A. Gray, Smithsonian Contr. Knowl. 5 (*Pl. Wright*. 2):77. 1853. *Conyza eriophylla* (A. Gray) Cronq., Bull. Torrey Bot. Club 70:632. 1943. TYPE: UNITED STATES. Arizona: [Cochise Co.], Sonoita Creek, Sep 1851, *C. Wright s.n.* (HOLOTYPE: GH!).

Short lived perennials from a slender but woody taproot, densely covered with a white, woolly indument. Stems 15-40 cm tall, sometimes much branched from the bottom third. Leaves often glabrate on the upper surface, eglandular, the basal and lower cauline oblanceolate, not clasping, sometimes slightly revolute, 2-3 cm long, 4-5 mm wide, shallowly serrate with 1-4 pairs of teeth on the distal margins, becoming linear, entire and gradually reduced in size upward. Heads 7-9 mm wide on peduncles mostly 1.5-4.5 cm long, in panicles or loose corymbs; phyllaries in 3-5 strongly graduated series, the innermost 5.5-7.0 mm long, the inner with a distal, narrowly elliptic, green, *Aster* like, central area between and above white, indurated zones, with purple apices, the margins hyaline. Pistillate corollas filiform, 4.5-5.0 mm long, the ligules erect, 0.5-0.8 mm long, purplish. Disc corollas glabrous or with a few hairs, 4.3-5.5 mm long, the tube 2.8-3.5 mm long, throat gradually ampliate, lobes 0.3-0.6 mm long, often purplish. Achenes elliptic-oblong, 2.1-3.0 mm long, 0.9-1.0 mm wide, strongly flattened, with 2, thick, white, marginal ribs, the faces tan, faces and margins sparsely to moderately but prominently long strigose, eglandular; pappus a series of 35-45 very slender, barbellate bristles 4.5-5.5 mm

long, sometimes with a few, inconspicuous, outer setae. Chromosome number unknown.

South central Arizona (Cochise and Santa Cruz counties) and west central Chihuahua (probably also in northeast Sonora); gravely soil in semidesert grassland, dry oak or pine-oak woodlands; 1000-2000 m; flowering July-October (-November).

To my knowledge, this paper is the first to report the occurrence of *Laennecia eriophylla* in México. A number of collections from western Chihuahua are known, and the species almost certainly occurs in Sonora, although I have not seen collections from there. Citations are provided from both the United States and México, because this species has been poorly known from both areas.

MÉXICO. Chihuahua: Mpio. Ocampo, Ocampo, mine site SW of town, sterile soils around hydrothermal outcrop, 1800 m, 26 Jul 1986, *Moore, et al. s.n.* (ARIZ); Parque Nacional de Cascada Basaseachic, more or less open, dry, *Pinus durangensis-Quercus hypoleucoides* woods in barranca to W of falls, on open rock, ca 1800 m, 14 Sep 1987, *Spellenberg 9310* (MEXU,NMC,TEX); Mpio. Temosachic, Nabogame, oak and oak-pine woodland, 1800 m, 1987 and 1988, *Laferrière 1570* (ARIZ), *1772* (TEX), *839* (TEX), & *2315* (TEX); 24.5 mi W of Basaseachic on Hwy 16, 4.2 mi E of Yepachic, large area of mostly bare, rock outcrops with scattered oaks, junipers, and manzanitas, 2010 m, 20 Aug 1984, *Nesom 5120* with P. Lewis (MEXU,NMC,TEX).

UNITED STATES. Arizona: Santa Cruz Co., Nogales to Ruby, 4300 ft, 25 Aug 1940, *Kearney & Peebles 14914* (ARIZ-2 sheets,LL); near Ruby, oak-grass association, 4300 ft, 2 Oct 1937, *Kearney & Peebles 13783* (ARIZ,LL); Pajarito Mts., 3.5 mi by jeep trail SE of Montana Peak, WSW of Yank Spring on Bald Spot at ridge top, W of Sycamore Canyon, 4480 ft, 22 Oct 1981, *Reichenbacher 909* (ARIZ); Atascosa Mts., 3.7 mi SE of Ruby on road to Peña Blanca Lake, 4350 ft, 21 Sep 1981, *Van Devender & Koppinger s.n.* (ARIZ).

In addition to the features noted in the key, *Laennecia eriophylla* is characterized by its phyllaries in 3-5 strongly graduated series, the inner with a distal, narrowly elliptic, green and "Aster like" central area, between and above the white, indurated zones.

7. *Laennecia flaginoides* DC., *Prodr.* 5:376. 1836. *Conyza flaginoides* (DC.) Hieron., *Bot. Jahrb. Syst.* 28:588. 1901. TYPE: MÉXICO. México: Environs de México, 16 Aug 1827, *Berlandier 820* (HOLOTYPE: G-DC, fide!; Isotypes: BM,G,GH!,P).

Heterochaeta stricta Benth., *Pl. Hartweg.* 206. 1845. TYPE: ECUADOR. Near Quito, *Hartweg 1145* (LECTOTYPE [Cuatrecasas by annotation, *fide* Zardini 1981] K; Isolectotypes: BM,GH!,NY,P). The Hartweg plant on the GH sheet is *Laennecia flaginoides*; achenes in the packet mounted directly below, are from *L. gnaphalioides*

and perhaps came from the plant of *L. gnaphalioides* (Holton s.n.) mounted on the same sheet.

Laennecia pinnatifida Turcz., Bull. Soc. Imp. Nat. Mosc. 24:178. 1851.

TYPE: ECUADOR. Near Quito, Aug 1846, Jameson 637 (Isotype: GH!).

Taprooted annuals, the whole plant densely white tomentose. Leaves linear-oblong, subclasping, shallowly toothed, glandular. Heads 5-6 mm wide, in a spike like panicle. Perfect flowers 3-10, strongly goblet shaped; pistillate corollas eligulate. Achenes obovate, basally acute, 1.2-1.6 mm long, 0.6-0.8 mm wide, usually purplish, completely covered by long, silky hairs, glandular; pappus biseriate, the outer a series of 34-40 short bristles 1.0-1.2 mm long, with ca 20 shorter and uneven bristles 1.0-1.2 mm long. Chromosome number $n=9$ pairs.

Baja California Sur, Sonora, Chihuahua, Durango, Zacatecas, Guanajuato, Jalisco, Michoacán, Aguascalientes, México, Hidalgo, Puebla, Nuevo León, San Luis Potosí, Veracruz, Oaxaca and Chiapas, Guatemala, and South America (Venezuela, Colombia, Ecuador and Perú); roadsides or meadows, often with pine or oak-pine; 1600-3100 m; flowering July-November.

8. *Laennecia gnaphalioides* (Kunth) Cass., Dict. Sci. Nat. 25:92. 1822. BASSONYM: *Conyza gnaphalioides* Kunth, Nov. Gen. Sp. Pl. 4[folio]:57. 1818; 4[quarto]:73, pl. 327. 1820. *Marsea gnaphalioides* (Kunth) Badillo, Bol. Soc. Ven. Cienc. Nat. 10:257. 1946. TYPE: VENEZUELA. Locis alsis montis Cocollar, *Humboldt & Bonpland s.n.* (HOLOTYPE: P, fiche!).

Laennecia parvifolia DC., Prodr. 5:376. 1836. TYPE: MÉXICO. México: Valle de Toluca, Oct 1827, Berlandier 1124 (HOLOTYPE: G-DC, fiche!; Isotype: P). This was included as a synonym of *L. gnaphalioides* by Cuatrecasas (1969) but of *L. filaginoides* by Zardini (1981).

Erigeron niveus Schultz-Bip., Bull. Soc. Bot. Fr. 12:85. 1865. TYPE: BOLIVIA. La Paz, Sorata, Feb-Mar 1858, Mandon 221 (HOLOTYPE: P; Isotypes: BM,F,G,GH,K,LP,NY).

Conyza evacioides Rusby, Bull. N.Y. Bot. Gard. 4:385. 1907. TYPE: BOLIVIA. Yungas, 1890, Bang 1875 (HOLOTYPE: NY; Isotypes: F,G,GH!,K,NY,US!).

Conyza pulcherrima M.E. Jones, Contr. W. Bot. 12:47. 1908. TYPE: MÉXICO. Chihuahua: Soldier Canyon, Sierra Madre Mountains, 16 Sep 1903, M.E. Jones s.n. (HOLOTYPE: POM; Isotypes: ARIZ!, BM,US!).

Similar in habit, vestiture and habitat to *Laennecia filaginoides* and often growing with it. Leaves entire to apically toothed, densely woolly, glandular. Heads 9-12 mm wide; phyllaries usually purple tipped. Pistillate corollas eligulate. Achenes light brown, often with a golden sheen, orbicular-obovate to obovate, usually with thick rib like margins, 1.5-2.0 mm long, 0.9-1.5 mm wide, margins fringed with long, silky hairs, each face with a central patch of hairs; pappus of 20-24 bristles, with an outer pappus a corona of laciniate, lanceolate scales (0.1-)0.3-0.6 mm high. Chromosome number $n=9$ pairs.

Chihuahua, Durango, Jalisco, Aguascalientes, Michoacán, México, San Luis Potosí, Veracruz, Oaxaca, Chiapas, disjunct to South America, where known from Venezuela, Colombia, Ecuador, Perú and Bolivia; clearings, wet meadows, grasslands or pastures, usually in areas of oak-pine, pine-juniper, or pine woods; 2000-2700(-3800 in South America) m; flowering August-November.

9. *Laennecia lasseriana* (Aristeg.) Nesom, *comb. nov.* BASIONYM: *Conyza lasseriana* Aristeg., in Lasser, *Fl. Venezuela* 10:287. 1964. TYPE: VENEZUELA. Mérida: Páramo de Los Leones, W of Mucuruba, 3500 m, May 1930, Gehriger 127 (HOLOTYPE: US!).

Perennials from a slender but woody base, the stems and leaves with a dense and close white tomentum obscuring the surface, also with sessile to short stipitate resin glands. Stems erect, 10-25 cm tall, often much branched. Leaves narrowly oblong to oblong-lanceolate, densely arranged, sessile to sub-clasping, sometimes slightly auriculate, 4-10 mm long, 0.5-2.0 mm wide, entire to shallowly toothed, particularly near the apex, margins often distinctly revolute. Heads 4-5 mm wide, sessile, in compact, terminal clusters of 2-5 or in short, narrow, spicate panicles; phyllaries reddish purple, sometimes with a discernible greenish central area and narrow midvein, the margins with a very narrow, hyaline edge but mostly not differentiated from the inner area, glandular but otherwise glabrate, narrowly triangular in 3-4 equal to subequal series, the inner 3.5 mm long. Pistillate corollas 1.8-2.2 mm long, eligulate, the stigma and styles extending 0.5 mm above the corolla. Disc corollas 3.0 mm long, the tube 2.0 mm long, the lobes cut to nearly the bottom of the limb. Achenes obovate to oblong-obovate, 0.8-1.0 mm long, with 2(-3) very thin nerves, sparsely strigose, minutely sessile glandular; pappus a single series of 14-16 slender bristles, 2.8-3.0 mm long at maturity.

Endemic to paramos in western Venezuela (state of Mérida); rocky slopes; ca 2700-3500 m; flowering January-May.

Laennecia lasseriana is recognized by its perennial duration, dense, white tomentum, narrow, short, densely arranged leaves, and reddish and glandular but otherwise glabrate phyllaries.

10. *Laennecia microglossa* (S.F. Blake) Nesom, *comb. nov.* BASIONYM: *Erigeron microglossus* S.F. Blake, *Contr. Gray Herb.*, n.s. 52:31. 1917.

Conyza microglossa (S.F. Blake) Cronq., Bull. Torrey Bot. Club 70:632. 1943. TYPE: MÉXICO. San Luis Potosí. Mountains near San Miguelito, Aug 1876. *Schaffner* 215 (HOLOTYPE: GH!).

Conyza dentonae McVaugh, Contr. Univ. Michigan Herb. 9:364. 1972. TYPE: MÉXICO. Jalisco: [Mpio. Ojuelos.] Grasslands near Km 18, SW of Ojuelos on the road to Aguascalientes, 15 Aug 1958, *McVaugh* 16974 (HOLOTYPE: MICH!).

Taprooted annuals, much branched from the base, the whole plant woolly. Leaves narrowly oblong-oblancheolate, shallowly toothed, clasping, glandular. Capitulescence open and diffuse; pistillate corollas with a ligule 0.2-0.4 mm long, about as long as the style branches. Achenes sparsely strigose, narrowly elliptic-oblancheolate, 1.1-1.7 mm long, 0.4-0.5 mm wide, with a few resinous glands near the apex, without prominently thickened margins; pappus of 13-17 bristles, biseriate but the outer series no more than a few setae. Chromosome number unknown.

Chihuahua, Durango, Zacatecas, Jalisco, and San Luis Potosí; grasslands or brushy plains, often with oaks, acacia, or cacti; 1800-2250 m; flowering May-September.

Laennecia microglossa is recognized by its annual duration, woolly vestiture, pistillate corollas with short ligules and essentially simple pappus of 13-17 bristles.

11. ***Laennecia mima*** (S.F. Blake) Nesom, *comb. nov.* BASIONYM: *Conyza mima* S.F. Blake, Contr. Gray Herb. 52:32. 1917. TYPE: VENEZUELA. Páramo de Mucuchieć (Mucuchies) Oct, *Moritz* 1404 in part (HOLOTYPE: B).

Taprooted annuals, erect, 5-30(-40) cm tall, the stems and leaves moderately to densely villous-tomentose with thin based trichomes, the surfaces not completely obscured, also with numerous, sessile, resin glands. Leaves narrowly oblong to oblong-lanceolate, densely arranged, 8-20 mm long, 2-4 mm wide, slightly auriculate, the margins shallowly toothed, particularly near the apex, less commonly entire, sometimes slightly revolute. Heads 4-6 mm wide, sessile to subsessile, rarely on pedicels 2-8 mm long, in spicate panicles; phyllaries glandular and sparsely villous with multicellular trichomes much thicker than elsewhere on the plant, narrowly ovate-lanceolate with broad, hyaline margins, in 2-3 equal to subequal series, the inner 4-5 mm long. Pistillate corollas eligulate, 1.8-2.1 mm long, the stigma and styles extending 0.3-0.5 mm above the corolla. Disc corollas 2.6-3.4 mm long, the tube 1.6-2.0 mm long. Achenes narrowly obovate to elliptic-obovate, 0.9-1.0 mm long, sparsely strigose, thin nerved; pappus a single series of 10-11 bristles 3.0-3.2 mm long at maturity.

Paramos in western Venezuela (state of Mérida); open, gravelly or rocky slopes, sometimes dominated by *Espeletia*; 3560-4200 m; flowering September-December.

Laennecia mima is recognized by its annual duration, villous-tomentose pubescence not completely obscuring the surfaces, narrow, mostly entire leaves, eligulate pistillate corollas and small, thin nerved achenes.

12. *Laennecia pimana* Nesom & Laferrière, *Phytologia* 68:202. 1990. TYPE: MÉXICO. Chihuahua: Mpio. Temosachic, 1 km E of Nabogame, 28 Oct 1988, J.E. Laferrière 2216 (HOLOTYPE: TEX!; Isotype: MEXU!).

Taprooted perennials. Leaves woolly above and beneath, mostly entire, not clasping. Heads in a spike like capitulescence, on peduncles 5-15 mm long; innermost phyllaries 6-7 mm long. Pistillate corollas eligulate. Disc corollas 4.3-5.0 mm long. Achenes obovate, 1.9-2.2 mm long, 0.8-1.0 mm wide, the faces tan, with thick, white, marginal ribs, glabrous except for a few sessile resin glands near the apex; pappus of 33-39 bristles, with an outer series of setae or bristles 0.3-0.5 mm long.

Known only from the vicinity of Nabogame in west central Chihuahua, México; pine-oak woods; 1800 m; September-November.

Laennecia pimana is recognized by its perennial duration, densely tomentose vestiture, eligulate pistillate corollas, large, glandular, but otherwise glabrous achenes with thick, marginal ribs and its biseriate pappus with numerous bristles.

13. *Laennecia prolialba* (Cuatr.) Nesom, *comb. nov.* BASIONYM: *Conyza prolialba* Cuatr., *Phytologia* 9:3. 1963. TYPE: COLOMBIA. Dist. Magdalena: Prados paramuños y rocosos entre las lagunas Naboda, Mamito, y Mamo, 4200-4300 m, 4 Oct 1959, Cuatrecasas & Romero-C. 24595 (HOLOTYPE: US!; Isotypes: COL,P).

Short lived perennials from a woody taproot. Sterile plants: forming low (3-5 cm high) mounds, with a dense, white tomentum completely obscuring the surfaces. Flowering plants: stems erect, 2-4(-6) dm tall, stems and leaves moderately to densely villous-tomentose with thin based trichomes, at least the leaves glabrescent and the surfaces not completely obscured, also with sessile to short stipitate resin glands. Cauline leaves lanceolate to oblong-lanceolate, slightly auriculate, subclasping, the margins sinuate to toothed, mostly 1-2(-3) cm long, 2-3(-5) mm wide. Heads 4-6 mm wide, sessile to subsessile or less commonly on pedicels to 5 mm long, in leafy, spicate panicles; phyllaries narrowly ovate-lanceolate with acuminate apices and broad, hyaline margins, glandular, villous with vitreous, thick based trichomes, in 2-4 equal to subequal series, the inner 4-5 mm long. Pistillate corollas 2.0-2.8 mm long, including the ligules 0.3-0.7 mm long. Disc corollas 3.0-3.5 mm long, the tube

2.0-2.2 mm long. Achenes obovate to narrowly obovate, thin nerved, tan to purplish, 0.8-1.1 mm long, glabrous or commonly very sparsely strigose with short, appressed hairs, eglandular or with glands clustered at the apex; pappus a single series of 10-17 bristles 2.6-3.0 mm long.

Colombia and Ecuador; open, rocky sites in paramo or subparamo, rarely lower in matorral; 2700-3900(-4300) m; flowering September-April.

Laennecia prolialba is very similar to *L. schiedeana*, and as noted by Cuatrecasas (1963), the two might reasonably be considered conspecific. The South American plants, however, are distinguished by their high elevation habitats, perennial duration and peculiar, mounded, densely tomentose growth forms in their nonflowering phases. The species is otherwise recognized by its pistillate corollas with short ligules, leafy, spicate panicles, glabrous or glabrate achenes, eglandular or glandular near the apex and with 10-15 pappus bristles.

14. ***Laennecia schiedeana*** (Less.) Nesom, *comb. nov.* BASIONYM: *Erigeron schideanus* Less., *Linnaea* 5:145. 1830. *Conyza schiedeana* (Less.) Cronq., *Bull. Torrey Bot. Club* 70:632. 1943. TYPE: MÉXICO. Veracruz: Llanos de Perote, Sep 1828, *Schiede 314* (B, *fide* Blake, 1917; Isotype seen by McVaugh 1984).

Conyza subdecurrens DC., *Prodr.* 5:379. 1836. *Erigeron subdecurrens* (DC.) Schultz-Bip. ex A. Gray, *Synopt. Fl. N. Amer.* 2(1):220. 1884. *Leptilon subdecurrens* (DC.) Small, *Man. Fl. S.E. U.S.* (ed. 2) 1371. 1913. TYPE: MÉXICO. Cordillera de Guchilapa, 20 Oct 1827, *Berlandier 1044 ex/14* (HOLOTYPE: G-DC, *fiche!*).

Conyza erythrolaena Klatt, *Jahrb. Hamburg Wiss. Anstalt* 10, 2:125. 1893. TYPE: MÉXICO. Michoacán: Hills near Patzcuaro, 21 Dec 1891, *Pringle 3984* (HOLOTYPE: B?; Isotypes: MEXU!, US-2 sheets!).

Erigeron subspicatus Benth. in Oerst., *Kjoeb. Vidensk. Meddel.* 82. 1852. *Conyza prolialba* Cuatr. var. *subspicata* (Benth.) Cuatr., *Phytologia* 9:5. 1963. TYPE: COSTA RICA. Volcán Irazu, *Oersted 268* (HOLOTYPE: K).

Leptilon integrifolium Woot. & Standl., *Contr. U.S. Natl. Herb.* 16:183. 1913. TYPE: UNITED STATES. New Mexico: Mogollon Mts., West Fork of the Gila River, 28 Aug 1903, *Metcalfe 610* (HOLOTYPE: US!).

Erigeron subspicatus Benth. var. *leiocarpus* S.F. Blake, *Brittonia* 2:337. 1937. TYPE: GUATEMALA. Sierra Cuchumatanes, alpine meadows, along trail between Huehuetenango and Soloma, 3260 m, 14 Sep 1934, *Skutch 1214* (HOLOTYPE: GH!).

Taprooted annuals 2-5(-10) dm tall, most of the plant moderately to densely covered with relatively thick, multicellular hairs, these immediately protracted into very long, filiform, crisped apices that produce a woolly-arachnoid pubescence, the hairs on the phyllaries continuing as thick and jointed for their whole length. Leaves lanceolate-oblong, 2-8 mm wide, entire to shallowly toothed near the apex or rarely shallowly lobed, clasping, with sessile to short stipitate, orange resin glands. Capitulescence usually a narrow, spike like panicle. Pistillate corollas with ligules 0.3-1.4 mm long. Achenes brown to slightly purplish, lustrous, sparsely short strigose to glabrous, oblong-obovate, 1.0-1.4 mm long, 0.4-0.7 mm wide, glandular near the apex or apparently sometimes eglandular, the ribs not thick or markedly differentiated in texture from the faces; pappus a single series of 15-20 bristles. Chromosome number, $n=9$ pairs.

Baja California Norte, Chihuahua, Sinaloa, [Coahuila?], Nuevo León, Michoacán, Guerrero, Guanajuato, San Luis Potosí, Hidalgo, Edo. México, Morelos, Puebla, Veracruz, apparently disjunct to Chiapas, Guatemala and Costa Rica, in the United States in New Mexico, Arizona, Colorado; fields, llanos, rocky hillsides, or meadows at timberline, in areas of pine, pine-oak, or fir, 1750-4000 m; August-November(-January).

A widespread species, highly variable in the amount of woolly pubescence and glandularity of the achene apex. It is distinctive, however, among the species with woolly pubescence in having some of the hairs continue as thick and multicellular for their whole length and in the conspicuous resin glands on the vegetative parts.

15. *Laennecia sophiifolia* (Kunth) Nesom, *comb. nov.* BASIONYM: *Conyza sophiifolia* Kunth, *Nov. Gen. & Sp.* 4[folio]:56. 1818; 4[quarto]:72, pl. 326. 1820. *Marsea sophiifolia* (Kunth) Badillo, *Bol. Soc. Venez. Cienc. Nat.* 10:256. 1946. TYPE: MÉXICO. [México]: Chalco, *Bonpland 4156* (HOLOTYPE: P, fide!; Isotype: F, fragment).

Conyza pulchella Kunth, *Nov. Gen. & Sp.* 4[folio]:56. 1818; 4[quarto]:72. 1820. TYPE: MÉXICO. México: Moran, *Humboldt & Bonpland 4104* (HOLOTYPE: P, fide!).

Conyza coulteri A. Gray var. *tenuisecta* A. Gray, *Synopt. Fl. N. Amer.* 1(2):221. 1884. *Eschenbachia tenuisecta* (A. Gray) Woot. & Standl., *Contr. U.S. Natl. Herb.* 16:186. 1913. TYPE: UNITED STATES. Arizona: Near Ft. Huachuca, 1882, *Lemmon s.n.* (HOLOTYPE: GII!).

Conyza serpentaria Grisebach, *Abhandl. Königl. Gesellsch. Wissens. Gott.* 24:176. 1879. As synonym *fide* Cabrera (1978).

Erect, taprooted annuals 3-7 dm tall, with stems, leaves and phyllaries papillate or stipitate resinous glandular and spreading hairy with coarse,

translucent, prominently multicellular hairs. Leaves once or twice pinnately dissected, not clasping. Heads 1.5-2.5(-3.5) mm wide, in an elongated, narrowly columnar to pyramidal panicle; phyllaries in 2-4 equal to subequal series, the inner 2.5-3.0 mm long, apices long acuminate and membranous. Pistillate corollas 0.8-1.2 mm long, eligulate. Disc corollas 2.2-2.6 mm long. Achenes 0.7-0.8 mm long, 0.3 mm wide, with thin nerves, very sparsely short strigose, minutely stipitate glandular; pappus a single series of 9-12(-15) bristles 2.5-3.0 mm long. Chromosome number, $n=9$ pairs.

Baja California Sur, Sonora, Sinaloa, Chihuahua, Durango, Nayarit, Jalisco, Michoacán, Zacatecas, Aguascalientes, Guerrero, Edo. México, Hidalgo, San Luis Potosí, Puebla, Veracruz, Oaxaca and Chiapas, Guatemala to El Salvador in Central America, and from there apparently disjunct to the Andean regions of South America in Colombia, Ecuador, Bolivia, Argentina, in the United States in Arizona, New Mexico and Texas; roadsides, clearings and other disturbed sites, desert flats, in areas of grassland, juniper, oak, pine; 1000-2700 m; flowering June-October.

Laennecia sophiifolia is very similar to high altitude *Laennecia artemisiifolia* from South America, but the former is strictly erect and has smaller heads and corollas. The plants of South America are clearly conspecific with those from North and Central America.

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I thank Drs. Billie Turner and Beryl Simpson for their review and comments on the manuscript, ARIZ, GH, MO, NMC and US for loans of specimens, and Dave Swofford, the author of PAUP, which offered analytic insights into even such a small set of data.

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FURTHER DEFINITION OF *CONYZA* (ASTERACEAE: ASTEREAE)

Guy L. Nesom

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

After the removal of *Laennecia*, New World *Conyza* is monophyletic, and a more meaningful and precise definition of the genus can be formulated. Among genera of New World Astereae, *Conyza* is more similar to *Erigeron* and *Trimorpha* in its phyllaries with orange resinous midveins and deltate disc corolla lobes, and more similar to *Trimorpha* than *Erigeron* in its 3 nerved phyllaries, broad zone of numerous pistillate flowers and pappus that elongates at maturity past the corollas. *Conyza* in the Old World appears to be polyphyletic.

KEY WORDS: *Conyza*, *Erigeron*, *Nidorella*, *Laennecia*, Astereae, Asteraceae.

The distinction between *Conyza* and *Erigeron* has long been problematic, but the problem has been accentuated by a lack of an understanding of the generic boundaries of *Conyza*. Zardini's definition of *Conyza* (1976) was largely a restatement of the traditional criteria used by Lessing (1832), DeCandolle (1836), Bentham (1873), Bentham & Hooker (1873) and Hoffmann (1890), and slightly broadened by Cronquist (1947). Cronquist correctly included in *Conyza* the ligulate species of *Erigeron* sect. *Caenotus*, but other ligulate species transferred to *Conyza* by him have now been included in *Laennecia* (Zardini 1981; Nesom 1990). With the removal of the superficially similar *Laennecia* (Nesom 1990), *Conyza* can be more precisely circumscribed.

In the traditional view, the pistillate flowers of *Conyza* have ligules absent or highly reduced, while the ligules in *Erigeron* are broad and prominent, usually extending well past the involucre. There are, however, other constant points of difference between these two genera, particularly in phyllary morphology, the relative composition of pistillate and hermaphroditic flowers, and length of the mature pappus bristles. As summarized in the key below, *Conyza* is more similar in features of pappus and floral morphology to *Trimorpha* (Nesom 1989b) than to *Erigeron*, although it is not clear whether the similarities represent homologies or features derived in parallel.

1. Phyllaries mostly 1 nerved; pistillate flowers in 1(-2-3) series, many fewer than the hermaphroditic ones; pappus bristles not elongating at maturity, not extending past the involucre *Erigeron*
- 1' Phyllaries mostly 3 nerved; pistillate flowers usually in numerous series in a broad zone, more numerous than the hermaphroditic ones; pappus bristles at maturity elongating past the involucre (2)
2. Pistillate flowers dimorphic and in 2 zones, eligulate in the inner zone, ligulate in the outer zone with the ligules extending past the involucre *Trimorpha*
- 2' Pistillate flowers monomorphic, the ligules absent or present but never more than barely exceeding the involucre in length . *Conyza*

As noted earlier (Nesom 1989a), a few species of *Erigeron* have 3 nerved phyllaries. They occur in each of the three species of *E. sect. Spinosi* and occasional species of the large *E. sect. Fruticosus*, as well as a few species of sect. *Wyomingia*. Because of the ubiquitous occurrence in both *Conyza* and *Trimorpha* of 3 nerved phyllaries, I believe this is a primitive feature in *Erigeron*. Some insular species of *Erigeron* have a greatly reduced number of disc flowers, so that the relative composition of ray and disc flowers is atypical and more like that of *Conyza*. Other species of *Erigeron*, particularly in sect. *Cincinnactis* produce extraordinarily large numbers of ray flowers with filiform ligules, which also shifts the ray/disc ratio. These exceptions do not alter significantly the associated groups of characters that distinguish *Conyza* from *Erigeron*.

This definition of *Conyza* holds for species of the New World, including the type, which appear to be monophyletic after the removal of *Laennecia*. In the Old World, however, the group of species currently identified as *Conyza* is more variably complex and includes species with 1 nerved phyllaries, yellow rays, glandular achenes and corollas, and other features that strongly suggest that a polyphyletic group is involved. The distinction between *Nidorella* and *Conyza* has been addressed by Wild (1969a; 1969b; 1975). In my opinion, however, this taxonomy is far from resolved and at least *Conyza* as now constituted in the Old World appears to be strongly heterogeneous, including species that probably belong with the species of *Nidorella*. Wild's overemphasis of the morphology of the ray florets, the relative degree of inclusion of the ray stigmas and the relative length of the mature pappus have contributed to the formation of an artificial classification.

Conyza welwitschii (S. Moore) Wild, *C. pyrrhopappa* Schultz-Bip. ex A. Rich., *C. ivaefolia* (L.) Less. and *C. stricta* Willd. all have glandular corollas and achenes. The first two have yellow ligules and *C. ivaefolia* has basally united pappus bristles. None of these can be accommodated in *Conyza* without

severely disrupting the natural boundaries of the genus. *Conyza aegyptica* (L.) Ait., *C. pinnata* (L. f.) Kuntze and *C. podocephala* DC. have eglandular achenes but their 1 nerved phyllaries set them apart from *Conyza* sensu stricto. Still others, such as *C. limosa* O. Hoffm., with disc flowers with sterile ovaries, and *C. tigrensensis* Oliv. & Hiern. and *C. subscaposa* O. Hoffm., with unusually large achenes, should also be suspected of representing clades divergent from *Conyza*. These examples of atypical variation among Old World species are representative but by no means complete.

The following generic description and list of representative species (both drawn from the New World) are provided as a step toward clarifying the definition of *Conyza*. The generic synonyms include New World and Old World taxa, and all are typified by species currently accepted at least by Old World systematists as *Conyza*. *Eschenbachia*, the oldest name representing Old World taxa, and *Dimorphanthus* have been formally rejected vs *Conyza* as generic names, but along with *Edemias*, *Marsea* and *Fimbrillaria*, they represent phylogenetically discordant elements within *Conyza* that probably will need to be segregated.

Conyza Less., *Syn. Gen. Comp.* 203. 1832, *nom. conserv.*, non Linnaeus.

Type species: *Conyza chilensis* Sprengel, *typus conserv.* (\equiv *Conyza primulaefolia* [Lamarck] Lourteig & Cuatr., according to Lourteig & Cuatrecasas 1985). *Erigeron* sect. *Conyza* (Less.) Baillon, *Hist. Pl.* 8:143. 1882.

Erigeron sect. *Caenotus* Nutt., *Gen. Plant.* 2:148. 1818. Type species:

Erigeron canadensis L. (\equiv *Conyza canadensis* [L.] Cronq.). *Conyza* sect. *Caenotus* (Nutt.) Cronq. *ex* Cuatr., *Webbia* 24:211. 1969.

The valid transfer of sect. *Caenotus* from *Erigeron* to *Conyza*, which has been attributed to Cronquist (Bull. Torrey Bot. Club 70:631. 1943), apparently was not made until Cuatrecasas' treatment of the Astereae of Colombia (1969).

Conyzella Fabric., *Enum.* (ed. 1) 86. 1759. Type species: *Erigeron canadensis* L. (\equiv *Conyza canadensis* [L.] Cronq.).

Leptilon Rafin., *Amer. Monthly Mag.* 268. 1818. Type species: *Leptilon divaricatum* (Michx.) Rafin. (\equiv *Erigeron divaricatum* Michx.; \equiv *Conyza ramosissima* Cronq.).

Eschenbachia Moench, *Method. Pl.* 573. 1794. Type species: *Eschenbachia globosa* Moench, *nom. illeg.* (\equiv *Conyza aegyptica* [L.] Ait.)

Dimorphanthus Cass., *Bull. Sci. Soc. Philom. Paris* 1818:30. 1818. Lectotype species (designated here): *Conyza* (*Erigeron*) *aegyptica* (L.) Ait. Cassini also cited *Erigeron siculum*, *E. gouanii* and *E. chinense*.

Edemias Rafin., *Fl. Tell.* 2:49. 1837. Lectotype species (designated here): *Conyza aegyptica* (L.) Ait. Rafinesque also cited "*Conyza gouani* L." (\equiv *C. gouanii* [L.] Willd.).

Marsea Adanson, *Fam.* 2:122. 1763. Type species: *Baccharis ivaefolia* L. (\equiv *Conyza ivaefolia* [L.] Less.)

Fimbrillaria Cass., *Bull. Sci. Soc. Philom.* Paris 31. 1818. Type species: *Baccharis ivaefolia* L. (\equiv *Conyza ivaefolia* [L.] Less.)

Annual or perennial herbs, nearly glabrous to coarsely hispid-pilose, sometimes stipitate glandular. Leaves alternate, entire to toothed or pinnately lobed. Heads campanulate-urceolate, in a terminal corymb or dense, ovoid panicle; phyllaries sometimes fused into a hypanthium like cup or ring and appearing inserted on it, the outer usually with 3, prominent, orange resinous nerves on the abaxial surface, the nerves apparently reduced to one in species with very small heads (e.g., *Conyza canadensis*). Pistillate flowers fertile, numerous in 1-4 series, the corollas whitish or bluish, tubular-filiform, usually shorter than the stigma, eligulate with a fimbriate apex or the ligules very short and not or barely exceeding the length of the involucre. Disc flowers relatively many fewer than the pistillate ones, perfect, fertile, the corollas light yellow, narrowly tubular-funnelform, with deltate lobes, eglandular; style branches with collecting appendages mostly deltate. Achenes biconvex with 2, thin, lateral nerves, glabrous to sparsely strigose with twin hairs (Zwilling-shaare), eglandular; pappus uniseriate, of barbellate bristles that lengthen to exceed the ray and disc corollas and involucre at maturity. Base chromosome number, $x=9$.

Representative New World species of *Conyza* sensu stricto examined.

Conyza apurensis Kunth, *C. blakei* (Cabrera) Cabrera, *C. bonariensis* (L.) Cronq., *C. canadensis* (L.) Cronq., *C. catharinensis* Cabrera, *C. coronopifolia* Kunth, *C. floribunda* (Kunth) Schultz-Bip., *C. microcephala* Hemsley, *C. notobellidiastrum* Griseb., *C. pampeana* (Parodi) Cabrera, *C. primulaefolia* (Lam.) Lourteig & Cuatr., *C. ramosissima* Cronq., *C. rivularis* Gardn., *C. saltensis* Cabrera, *C. sordescens* Cabrera, *C. trihecatactis* (S.F. Blake) Cuatr., *C. uliginosa* (Benth.) Cuatr. and *C. burkartii* Zardini.

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TAXONOMIC OVERVIEW OF *BRICKELLIA COULTERI* (ASTERACEAE: EUPATORIEAE), INCLUDING *B. BRACHIATA* AND *B. MEGALODONTA*

B.L. Turner

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

Brickellia coulteri, a species of northeastern México and adjacent U.S.A., is comprised of three, largely allopatric, regional varieties: var. **adenopoda** (B.L. Robins.) B. Turner (which includes *B. megalodonta* Greenm.); var. **brachiata** (A. Gray) B. Turner; and var. **coulteri**. The var. *adenopoda* occurs in southern Baja California and southern Sonora, southward along the Pacific slopes to Michoacán; var. *brachiata* largely occurs in the more montane portions of northeastern Sonora, Chihuahua, Coahuila and adjacent U.S.A.; var. *coulteri* is largely confined to the lower elevations of the Sonoran Desert Regions of Baja California and eastern Sonora. At or near regions of contact, intergradation occurs.

KEY WORDS: *Brickellia*, Asteraceae, Eupatorieae, México.

Brickellia coulteri is a commonly collected species of northeastern México and closely adjacent U.S.A. Robinson (1917) recognized *B. coulteri* as a widespread, highly variable species, without infraspecific categories, although he did recognize a typical "forma," which included those plants with glandular hairs on the ultimate peduncles, and a "forma" *eglandescens*, which he applied to those plants having crisp eglandular hairs on the peduncles. McVaugh (1972; 1984) reduced *B. megalodonta* (which Robinson recognized) to varietal status under *B. coulteri*, and in the present paper, I have reduced Gray's *B. brachiata* to varietal status. The latter is largely composed of those plants referred to by Robinson as "forma *eglandescens*" and occurs primarily in the interior montane portions of the Sonoran and Chihuahuan deserts. These several taxa are largely allopatric and intergrades between them occur, including forms with both glandular and eglandular hairs intermixed.

In my forthcoming treatment of *Brickellia* for México, I will recognize three regional varieties within *B. coulteri*, as indicated in the key that follows and by the distributional maps shown in Figure 1. The latter was largely compiled from approximately 200 sheets, most of these deposited at LL and TEX, but also includes specimens housed at GII and WIS. The Mexican states indicated in the keys and elsewhere are abbreviated by the first three letters of the states concerned.

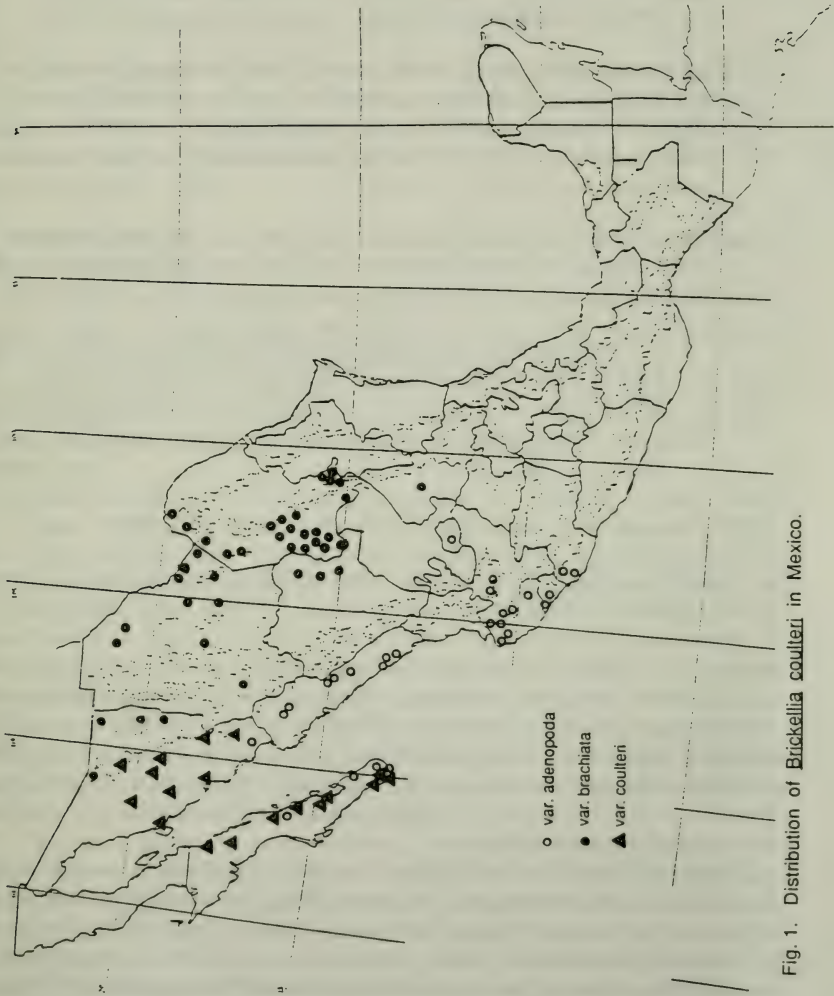


Fig. 1. Distribution of *Brickellia coulteri* in Mexico.

Brickellia coulteri A. Gray, *Pl. Wright*. 1:86. 1852.

Three varieties recognized as follows:

1. Mid stem leaves on primary stems mostly 2-4(5) cm long; capitulescence of erect or narrowly ascending branches, the ultimate peduncles mostly 0.5-1.5(2.0) cm long; peduncles usually without glandular hairs, sometimes intermixed with both glandular and eglandular hairs or rarely glandular throughout; ne Son, Chi, Coa, Dur var. *brachiata*
- 1' Mid stem leaves on primary stems mostly 4-6 cm long; capitulescence of broadly to widely ascending branches, the ultimate peduncles mostly 1.5-4.0 cm long; peduncles mostly glandular pubescent, rarely not . (2)
 2. Florets mostly 8-12 per head; peduncles widely divergent, mostly 2-4 cm long; s Baj, s Son, Sin, Dur, Nay?, Jal, Col, Agu and Mic var. *adenopoda*
 - 2' Florets mostly 13-21 per head; peduncles mostly ascending, 1.5-2.5 cm long; n Baj, s Baj, w Son var. *coulteri*

Brickellia coulteri A. Gray var. *coulteri*. *Pl. Wright*. 1:86. 1852.

Found in n Baj, s Baj, Son and adjacent U.S.A., mostly in the Sonoran Desert regions, dry hillsides and sandy washes, 10-1000 m; October-March.

Sprawling, brittle stemmed shrub or shrublet to 1 m high; mid stem leaves mostly 4-6 cm long, 3-4 cm wide; petioles mostly 1-3 cm long; blades more or less hastate, sparsely pubescent to glabrate; heads mostly in open terminal cymes, the ultimate peduncles usually ascending, 1.5-2.5 cm long, mostly glandular pubescent, or these intermixed with nonglandular hairs; involucre turbinate, the bracts usually abruptly apiculate, rarely not; florets 13-22 per head; achenes 3-4 mm long, the pappus of 35-45 white bristles 5-7 mm long; chromosome number, $n=9$ pairs.

Southward along the Pacific slopes, the variety grades into var. *adenopoda*; to the east, it grades into var. *brachiata*. Type material of this taxon was presumably collected in Baja California by Coulter (no. 273). Two heads of the holotype are to be found in a packet at GIL. The heads are borne on glandular peduncles and each contained about 20 florets (as determined by receptacular scars). In northern Sonora, this variety grades into var. *brachiata*; indeed, I would call most of the specimens in Arizona var. *brachiata*, those in the southwestern part of the state showing considerable gradation toward var. *coulteri*.

Brickellia coulteri A. Gray var. ***adenopoda*** (B.L. Robins.) B. Turner, *comb. nov.* BASIONYM: *Brickellia brachiata* A. Gray var. *adenopoda*

B.L. Robins., Mem. Gray Herb. 1:63. 1917. TYPE: MÉXICO. Sinaloa: vicinity of San Blas, 24 Mar 1914? (year not legible), *J.N. Rose, et al.* 13374 (Fragment of holotype: GH!; Isotype: GH!).

Brickellia megalodonta Greenm., Proc. Amer. Acad. Arts 40:34. 1904.
Brickellia coulteri A. Gray var. *megalodonta* (Greenm.) McVaugh,
Contr. Univ. Michigan Herb. 9:378. 1972. TYPE: MÉXICO.
Jalisco: Guadalajara, 22 Sep 1903, *E.W.D. Holway* 5022 (HOLO-
TYPE: GH!).

Found in s Baj, s Son, Sin, Nay?, Jal, Col, Agu and Mic, mostly Pacific slopes in tropical deciduous forests, 0-1600 m; October-January.

McVaugh reduced this taxon to varietal rank without recognition that the earlier epithet, var. *adenopoda*, was available. He correctly noted the range if the taxon, however, and most of the characters that marked it.

Specimens from Baja California (Figure 1), mostly on deposit at GH, have more stiffly divaricate branches in the capitulescence, otherwise there is little else to distinguish these from their mainland counterparts.

Brickellia coulteri A. Gray var. *brachiata* (A. Gray) B. Turner, *comb. nov.* BASIONYM: *Brickellia brachiata* A. Gray, Proc. Amer. Acad. Arts 21:385. 1886. TYPE: MÉXICO. Chihuahua: San Miguel, 27° 01' N, 107° 38' W (McVaugh 1977), Aug-Nov 1885, *Edward Palmer* 169 (HOLOTYPE: GH!).

Found in ne Son, Chi, Coa, Dur, n Zac?, San and adjacent U.S.A., mostly Sonoran and Chihuahuan deserts in dry rocky soils, 700-2000 m; all seasons.

Erect divaricately branched shrublet or shrub to 1.5 m high; much resembling var. *coulteri*, but the leaves mostly smaller and the ultimate peduncles mostly shorter with usually eglandular hairs (rarely with glandular trichomes throughout); chromosome number, $n=9$ pairs.

The variety grades into var. *coulteri* to the northwest, especially in the adjacent regions of the U.S.A. Robinson (1917) retained this taxon as a species but added to it the var. *adenopoda*. Actually, the var. *brachiata* is closer to var. *coulteri* than the latter is to var. *adenopoda*, there being considerable intergradation between these in northern Sonora and southern Arizona. *Brickellia coulteri* var. *adenopoda* intergrades with var. *coulteri* in southern Sonora and adjacent Sinaloa. It should also be mentioned that the involucre of the type specimen of var. *brachiata* is rather unusual of the variety, in that the outer bracts are somewhat scarious and compact with obtuse apices. Nearly similar involucre bracts occur sporadically over the range of the species.

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BOOK REVIEWS

Michael J. Warnock

Department of Biological Sciences, Sam Houston State University,
Huntsville, Texas 77341 U.S.A.

Mosses Lichens & Ferns of Northwest America Dale E. Vitt, Janet E. Marsh & Robin B. Bovey. Lone Pine Publishing, 414, 10357 109th St., Edmonton, Alberta, Canada T5J 1N3 (available in the United States through University of Washington Press, P.O. Box 50096, Seattle, WA 98145-5096, USA. 1989, 296 pp., \$17.50, paper. ISBN 0-295-96666-1.

This volume is a handy field guide for a region that abounds in bryophytes, lichens and ferns. It is of a size conducive for field use. However, its paper cover may not withstand extensive field use and exposure to moisture. Liverworts are also included in the work, even though not mentioned in the title. While not every species of these plant (here broadly used to include lichens) groups that grows in northwestern North America is included, the more common and most likely encountered taxa are represented in this book. The book has been designed for ease of use, with each large group (mosses, liverworts, lichens, and ferns and allies) treated separately, and groupings of taxa with similar features within each of these larger groups. The ease of use is intended to make the book useful for amateurs, but the information contained in the work makes it useful as well, for individuals with more formal training in plant systematics.

Introductory discussions are present for the area covered by the book and for each of the plant groups. The vegetation zones found on the vegetation zone maps appear to have some inaccuracies, particularly for Alaska, but the descriptions of the vegetation zones as they apply to the distribution of the plants are good. Most taxa treated are accompanied by a photograph, a description, a range map and a set of symbols to represent the ecological distribution of the plant. Other taxa are mentioned in the text of fully treated taxa. Information accompanying these additional taxa varies from nearly complete to scanty. The photographs are excellent aids to verify identifications from the keys. The keys appear to be workable and to stress as far as possible, the macroscopic features of the plants. While I am not familiar enough with the bryophytes or lichens to make a judgment, there appears, for the ferns at least, to be some emphasis on the Canadian representatives of the groups treated, at the expense of plants from Alaska, Idaho, Montana, Oregon and Washington.

Overall, I find the book quite useful for workers who might wish to identify cryptogams from the northwestern United States, but are not specialists in these groups of plants. Of course, specialists will rely on the more technical works on these organisms (cited in the introductory material to this book).

Land Above the Trees A Guide to American Alpine Tundra. Ann H. Zwinger & Beatrice E. Willard. The University of Arizona Press, 1230 N. Park Ave., Suite 102, Tucson, AZ 85719-4140, USA. 1989, xvii, 487 pp., \$16.95, paper. ISBN 0-8165-1110-1.

Although this book is not a scientific treatise on alpine tundra, it is an interesting book to read, containing considerable information presented in a manner to make it easily understood. Information presented is largely anecdotal from personal experiences and observations of the authors. One is led to believe from the title, that tundra in all the Americas might be included. However, the scope of this book is limited to treatment of tundra areas in the contiguous United States. The first section of the book contains descriptions of the tundra environment, along with some geological history and descriptions of different types of plant communities that may be found in tundra. The main portion of the text describes in more detail, tundra in various areas. Although eight distinct areas of tundra are delimited on the map in the introductory material, only six of these are discussed at length in the text. Some inconsistencies appear on the map as regards placement and extent of tundra areas in the United States. Some of these inconsistencies are due to the difficulty of trying to plot a very small area on a large scale map, but others, such as the tundra area placed in northeastern Arizona, simply do not exist as far as I am aware. Most of the text describing particular tundra areas is devoted to the Southern Rocky Mountains and Sierra Nevada regions, those with which the authors apparently are most familiar. Throughout the text, drawings (mostly of plants) by the senior author are found. Most of the drawings are reasonably accurate and could be used by comparison, to identify a plant. However, no keys to the plants are found, and one would need to leaf through the entire book to attempt to find the proper drawing to match an unknown plant. Probably the most scientifically useful part of the book is a list of plant species, when they flower and where they are found. Even here, some inaccuracies are found, and authors are not listed with the Latin names.

In short, the book is quite readable, and even with the difficulties cited above, could be recommended for anyone wishing to learn more about alpine tundra on an informal basis.

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Information for Authors

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Authors should arrange for two workers in the appropriate field to review the manuscript before submission. Copies of reviews should be forwarded to the editor with the manuscript. Manuscripts will not be published without review.

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